

A REVISION OF THE GENUS *ASPIDOSIPHON* (SIPUNCULA: ASPIDOSIPHONIDAE)

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Abstract. — The 64 putative species of the sipunculan genus *Aspidosiphon* and the morphological characters used to differentiate them are critically reviewed. The monograph of Stephen & Edmonds (1972) is used as a starting place and all changes made in the intervening years are reiterated here. All available type material was studied and new collections of Hawaiian and Caribbean material are used to analyze within-deme variation. Hook and anal shield morphology are determined to be broadly useful at the species level, four characters (longitudinal muscle layer, retractor muscle origins, caudal shield, nephridia length) in a more restricted manner to separate subgroups, and three (introvert/trunk angle, bifurcated anterior spindle muscle, loosely wound gut coil) are useful in special cases. A new subgenus, *Aspidosiphon (Akrikos)*, is proposed for those five species lacking hooks in rings. A key to, and a discussion of, the 19 remaining species (plus one reduced to subspecies) with the newly designated synonyms are presented. A brief statement of the distribution of each species is given. An overall summary of the zoogeography and habitat shows more endemic species are found in the warm water regions of the Atlantic Ocean than in the Indo-West Pacific, and that only 42% of *Aspidosiphon* species live in coral or rock.

This continues our revisionary series on the species of sipunculan worms (e.g., Cutler & Cutler 1985a, b, 1986, 1987b, 1988). With this work we complete our examination of all the genera in this phylum except *Phascolosoma*, which is in preparation. The monograph of Stephen & Edmonds (1972) is the starting place for this work (48 species names). Also included (Table 1) are the 11 species erected since that time, the two species transferred into this genus, and the three resurrected names.

The genus *Aspidosiphon* was erected by Diesing in 1851, and was placed in its own family, *Aspidosiphonidae*, by Baird (1868) in the order *Aspidosiphoniformes* Cutler & Gibbs (1985). The name *Paraspidosiphon* was proposed by Stephen in 1964 as a genus for those species with the longitudinal muscle layer separated into bundles. Cutler (1973) reduced it to subgeneric rank and this

has been followed by most other authors (see discussion below).

Whenever possible we have obtained type material to verify the original descriptions. In several cases we have made detailed observations on series of recently collected individuals to evaluate better the traditionally used morphological characters. Recent collecting trips to Hawaii, Curacao and Venezuela (Cumana and Isla de Los Roques) have greatly facilitated this effort. The opportunity to observe living material is invaluable. Parts of these collections will be deposited in the National Museum of Natural History, Washington, D.C. as reference material.

We first discuss the morphological characters in light of our recent analyses, then discuss those taxa not clearly belonging to this genus. Following are a key to all the species we consider valid, a section where

each of these species is discussed including a synonymy, a discussion of any newly added junior synonyms, and a summary of the known distribution of each species. A short zoogeographical summary of the genus concludes this work.

For clarity in the Morphological Characters section, the recent work of Saiz Salinas (1984) needs to be mentioned here. His redescription of Quatrefages' 1865 species from the Paris Museum has led to the elevation of *A. coyi* and *A. laevis* as senior synonyms of the more familiar *A. truncatus* for the former and the large *A. cumingii/klunzingeri* complex for the latter. In both cases holotypes are now available to science, which is not the case for the more familiar names. In some ways this action is analogous to that of Rice & Stephen (1970) where they resurrected the older and long unused names of Gray and Baird.

The following abbreviations are used in the text for the museums from which we borrowed material: American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum für Naturkunde der Humboldt-Universität zu Berlin (MNHU); Musée Océanographique Monaco (MOMV); Naturhistoriska Riksmuseet, Stockholm (NHRS); Royal Scottish Museum, Edinburgh (RSME); National Museum of Natural History, Washington (USNM); Zoologisk Museum, Copenhagen (UZMK); Zoological Institute, Academy of Science, Leningrad (ZIAS); Zoological Institute, Tohoku University, Sendai (ZITU); Zoologisch Museum, Universiteit van Amsterdam (ZMUA); Zoological Museum, University Bergen (ZMUB); Zoologisches Museum, Universität Hamburg (ZMUH).

Morphological Characters

1. Introvert hooks and spines.—As in most genera, the introvert bears (in all but three species) some array of specialized structures

usually referred to as hooks. Voss-Foucart et al. (1977) have shown these to lack chitin but consist of a horny protein. Many hooks are arranged in regular rings around the distal portion of the introvert and may have either one or two points (uni- or bidentate). On some species scattered hooks also are found proximally and in two species only scattered hooks are found. Additionally, epidermal structures of varying sizes and shapes called spines are arranged in a random manner on the proximal portion of the introvert. Examination of the literature reveals that the term "spine" meant different things to different authors, sometimes being used as a synonym for what others would term "unidentate hook." Since hooks and spines come in a wide variety of arrangements, sizes, and shapes, and often grade into one another, it is easy to understand the genesis of this problem that is unique to *Aspidosiphon*. We will attempt some clarification and definitions.

In the phylum Sipuncula, the term "hook" has been applied to structures having a wide variety of shapes, sizes, and arrangement. It is clear that a *Themiste* hook is different from a *Nephasoma* hook and that both differ from *Phascolosoma* hooks. Structures that have been called "spines" are similar to "hooks" of *Themiste* and of some *Phascolion* species. We now propose calling all of these introvert structures hooks. The term "spine" will be restricted to conical pointed anal shield units. The hook's apex points posteriorly (away from the mouth) with the convex curvature being anterior.

The different types of hooks are defined as follows:

Type A: *Compressed hooks.*—Usually arranged in rings, occasionally scattered, laterally compressed, and having, in a side view, a distinct posterior curve. These may be unidentate or bidentate (Fig. 1A, B). When a secondary tooth is present it may be variable in size, sometimes reduced to a

Table 1.—Original and proposed names of the *Aspidosiphon* species.Subgenus *Aspidosiphon* s.s.

<i>Aspidosiphon albus</i> Murina, 1967	no change*
<i>Aspidosiphon brocki</i> Augener, 1903	<i>A. elegans</i>
<i>Aspidosiphon carolinus</i> Sato, 1935	<i>A. elegans</i>
<i>Aspidosiphon cylindricus</i> Horst, 1899	<i>species inquirenda</i>
<i>Aspidosiphon elegans</i> (Chamisso & Eysenhardt, 1821)	no change
<i>Aspidosiphon exhaustus</i> Sluiter, 1912	<i>A. muelleri</i>
<i>Aspidosiphon exiguus</i> Edmonds, 1974	no change
<i>Aspidosiphon exilis</i> Sluiter, 1886	<i>A. elegans</i>
<i>Aspidosiphon gerouldi</i> ten Broeke, 1925	<i>A. misakiensis</i>
<i>Aspidosiphon gosnoldi</i> Cutler, 1981	no change
<i>Aspidosiphon gracilis</i> (Baird, 1868)	no change
<i>Aspidosiphon hartmeyeri</i> Fischer, 1919	<i>A. misakiensis</i>
<i>Aspidosiphon hispitrofus</i> LiGreci, 1980	<i>A. muelleri</i>
<i>Aspidosiphon homomyarius</i> Johnson, 1964	<i>A. elegans</i>
<i>Aspidosiphon imbellis</i> Sluiter, 1902	<i>A. muelleri</i>
<i>Aspidosiphon inquilinis</i> Sluiter, 1902	<i>A. muelleri</i>
<i>Aspidosiphon jukesii</i> Baird, 1873	<i>A. muelleri</i>
<i>Aspidosiphon kovaleskii</i> Murina, 1964	<i>A. muelleri</i>
<i>Aspidosiphon longirhyncus</i> Cutler & Cutler, 1980	<i>A. mexicanus</i> *
<i>Aspidosiphon macer</i> (Sluiter, 1891)	<i>species inquirenda</i>
<i>Aspidosiphon mexicanus</i> (Murina, 1967)	no change*
<i>Aspidosiphon misakiensis</i> Ikeda, 1904	no change
<i>Aspidosiphon muelleri</i> Diesing, 1851	no change
<i>Aspidosiphon ravus</i> Sluiter, 1886	<i>A. elegans</i>
<i>Aspidosiphon spinalis</i> Ikeda, 1904	<i>A. elegans</i>
<i>Aspidosiphon spinosus</i> Sluiter, 1902	<i>A. elegans</i>
<i>Aspidosiphon spiralis</i> Sluiter, 1902	no change
<i>Aspidosiphon thomassini</i> Cutler & Cutler, 1979	no change*
<i>Aspidosiphon tortus</i> Selenka, de Man & Bülow, 1883	<i>A. muelleri</i>
<i>Aspidosiphon venabulum</i> Selenka, de Man & Bülow, 1883	no change*
<i>Aspidosiphon zinni</i> Cutler, 1969	no change*

Subgenus *Paraspidosiphon*

<i>Aspidosiphon ambonensis</i> Augener, 1903	<i>A. tenuis</i>
<i>Aspidosiphon angulatus</i> Ikeda, 1904	<i>A. laevis</i>
<i>Aspidosiphon brasiliensis</i> Cordero & Mello-Leitao, 1952	<i>A. laevis</i>
<i>Aspidosiphon coyi</i> Quatrefages, 1865	no change
<i>Aspidosiphon cumingii</i> Baird, 1868	<i>A. laevis</i>
<i>Aspidosiphon exostomus</i> Johnson, 1964	<i>A. steenstrupii</i>
<i>Aspidosiphon fischeri</i> ten Broeke, 1925	no change
<i>Aspidosiphon formosanus</i> Sato, 1939	<i>A. tenuis</i>
<i>Aspidosiphon gigas</i> Sluiter, 1884	<i>A. laevis</i>
<i>Aspidosiphon grandis</i> Sato, 1939	<i>A. laevis</i>
<i>Aspidosiphon havelockensis</i> Haldar, 1978	<i>A. tenuis</i>
<i>Aspidosiphon insularis</i> Lanchester, 1905	<i>Phascolosoma perlucens</i>
<i>Aspidosiphon johnstoni</i> Edmonds, 1980	<i>A. laevis</i>
<i>Aspidosiphon klunzingeri</i> Selenka, de Man & Bülow, 1883	<i>A. laevis</i>
<i>Aspidosiphon laevis</i> Quatrefages, 1865	no change
<i>Aspidosiphon levis</i> Sluiter, 1886	<i>A. tenuis</i>
<i>Aspidosiphon major</i> Vaillant, 1871	<i>A. laevis</i>
<i>Aspidosiphon makoensis</i> Sato, 1939	<i>A. steenstrupii</i>
<i>Aspidosiphon ochrus</i> Cutler & Cutler, 1979	<i>A. steenstrupii</i>
<i>Aspidosiphon pachydermatus</i> Wesenberg-Lund, 1937	<i>A. laevis</i>
<i>Aspidosiphon parvulus</i> Gerould, 1913	no change

Table 1.—Continued.

<i>Aspidosiphon planoscutatus</i> Murina, 1968	no change
<i>Aspidosiphon quatrefagesi</i> Saiz Salinas, 1984	<i>A. laevis</i>
<i>Aspidosiphon pygmaeus</i> Fischer, 1921	<i>A. muelleri</i>
<i>Aspidosiphon schnehageni</i> Fischer, 1913	<i>A. gracilis schnehageni</i>
<i>Aspidosiphon semperi</i> ten Broeke, 1925	<i>A. steenstrupii</i>
<i>Aspidosiphon speciosus</i> Gerould, 1913	<i>A. laevis</i>
<i>Aspidosiphon speculator</i> Selenka, 1885	<i>A. steenstrupii</i>
<i>Aspidosiphon spinoscutatus</i> Fischer, 1922	<i>A. parvulus</i>
<i>Aspidosiphon steenstrupii</i> Diesing, 1859	no change
<i>Aspidosiphon tenuis</i> Sluiter, 1886	no change
<i>Aspidosiphon trinidadensis</i> Cordero & Mello-Leitao, 1952	<i>A. steenstrupii</i>
<i>Aspidosiphon truncatus</i> (Keferstein, 1867)	<i>A. coyi</i>
<i>Golfingia mokyevskii</i> Murina, 1964	<i>Antillesoma antillarum</i>

* Now in new subgenus *A.* (*Akrikos*).

small knob. A transition zone in some species exists at the proximal end of the rings of hooks where one may find a gradual widening of the anterior base of the unidentate hooks. Sometimes these scattered hooks are rounded at the anterior-lateral corners but still compressed posteriorly looking like a ship's stout mast and sail.

Type B: *Pyramidal hooks*.—Have triangular bases, the anterior side of which is shorter than the lateral sides, are usually less curved than Types A or C, are variably pigmented (dark to light), and translucent (Fig. 1E, F). The borderline between Types A and B is not clear in all species.

Type C: *Conical hooks*.—Have a nearly circular cross section (cone shape), a gentle posterior curve, and are usually opaque and dark colored (Fig. 1C, D). This type is found on the dorsal side of *A. elegans*' introverts.

When introvert skin is removed and placed on a slide in a drop of glycerin for closer examination, the orientation of these hooks can add to the confusion. If viewed from the anterior or posterior (instead of laterally), scattered unidentate compressed hooks look very much like pyramidal hooks (Fig. 1G). However, a compressed hook has

a narrower base. Further distortion can be caused if the hooks are not lying flat on the slide. Scanning electron micrographs can help reveal the natural configurations and the three dimensionality of these structures.

The shape of the clear area (less dense to transmitted light) in the hook has limited taxonomic value. In most species there is an ill-defined triangular area, but in *A. steenstrupii* and *A. elegans* there is a thin, posteriorly directed, tongue-like extension (Fig. 2).

The height of the hook has sometimes been used as a diagnostic character, but this has limitations. The unidentate *A. laevis* complex (as defined below) shows a clear correlation between trunk size and hook size (5–10 mm worms have 20–40 μm hooks, 20–30 mm worms have 40–60 μm hooks, and 40–70 mm worms have 60–80 μm hooks). The same pattern is shown by an analysis of 32 specimens of *A. steenstrupii* ranging in trunk length from 7–50 mm. Hook size varied from 30–90 μm with larger worms having larger hooks (a linear regression of these data gave a positive slope of 0.89). Therefore, hook size should not be considered in isolation from trunk size. Despite this a clear pattern does appear with certain species (e.g., the members of the new subgenus proposed here) always having small hooks (under 30 μm) and some species

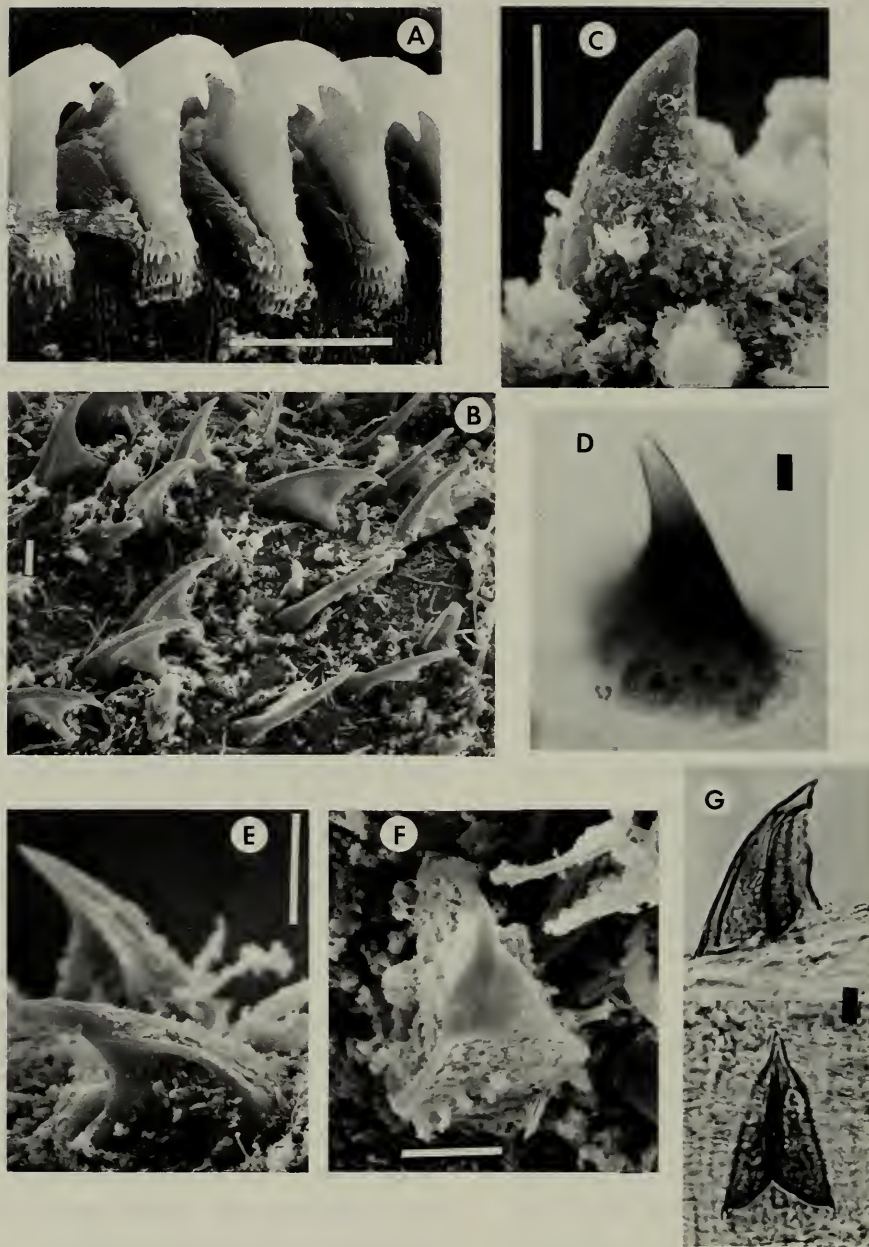


Fig. 1. Introvert hooks: A, Compressed, bidentate (Type A) from *A. muelleri*, posterior view; B, Compressed unidentate (Type A) from *A. misakiensis*; C–D, Conical (Type C) from *A. elegans*; E, Pyramidal (Type B) from *A. parvulus*; F, Pyramidal (Type B) from *A. steenstrupii* viewed from above; G, Pyramidal (Type B) from *A. steenstrupii*, different angles on light microscope. Scale line = 10 μm , for G = 20 μm .

with only larger hooks. The central problem is that many species have both large and small hooks.

In general, some species lack unidentate hooks, some lack bidentate hooks, some have both Type A and B hooks while others have only Type A hooks. Certain species will have both kinds of compressed and Type B hooks. In summary, if one examines the most distal rings of hooks and differentiates between unidentate Type A and Type B

hooks, hook morphology can be useful to the systematist in almost all cases and hook size can help in some cases.

2. *Anal shield (degree of development, nature of units, grooves).*—At the anterior end of the trunk, horny protein (not chitin) forms an array of cuticular units varying in degree of development (Voss-Foucارت et al. 1977). At one extreme is *A. mexicanus* or *A. thomassini* with a collection of small scattered units sometimes looking more like an area



Fig. 2. Internal hook structure: A, *A. elegans*, B, *A. steenstrupii*, C, *A. tenuis*. Note absence of tongue-like extension in C. Scale lines = 20 μm .

of rough skin. At the other end of the continuum is *A. laevis* or most *A. muelleri* where the units are compacted to form a thick, dark, solid mass. These two species are among those that have shields with well developed longitudinal and/or transverse grooves. When a shield has aggregations of units separated by grooves we refer to these aggregations as plates. The shield nearest the mid-dorsal anus is the dorsal part while that nearest the introvert is the ventral part.

The nature of the shield units may undergo slight changes with age (see *A. jukesii* in Cutler & Cutler 1979a:970) and may be modified by the size/shape of the shell (gastropod vs. scaphopod) or other space occupied by the worm. When the introvert is retracted this shield functions as an operculum. While some within-deme variation does exist, the morphology of the anal shield is consistent enough and distinct enough to be useful to the systematist.

3. *Caudal shield (degree of development)*.—At the posterior end of the trunk there is an epidermal structure (horny protein) present in most (but not all) species. This shield assumes various forms in living worms and, therefore, when preserved, can also vary from rather flat to pointed to pagoda shaped. They have a variable number of radially arranged grooves or furrows, but this attribute is not species specific. Even within a deme the degree of development

(thickness) varies (Fig. 3). In a species with extensive historical data indicating a “normal” shield, one may find individuals with very weakly developed shields. In such animals the shield may be reduced to some papillae and only a vague suggestion of a chitinous layer. It is probable that in many species the genetic potential is there, but its expression is variable and responds to environmental stimuli or age. Some species (*A. laevis*) always have a shield and others (e.g., *A. mexicanus* or *A. zinni*) never do. When a shield is present, there is little to distinguish one species from another using this character. Therefore, aside from presence/absence, the caudal shield has limited value to the systematist.

4. *Introvert retractor muscles (origin, degree of fusion)*.—The single pair of long muscles used to retract the introvert insert at the anterior end and originate from the ventral trunk wall in the posterior third of the worm. The placement of these origins (attachment) is usually included in species descriptions, often with a significant lack of precision (near the posterior end, in the last quarter), but sometimes it is used as a diagnostic (or key) character. While in other genera we have found that retractor origins appear to shift anteriorly as the animal grows (zone of trunk growth being posterior to the origins), it is difficult to generalize about this in *Aspidosiphon*. If one calculates the dis-



Fig. 3. Caudal shields of *A. elegans*. Three 17 mm worms from one deme in Ponape to show variation in degree of development. Scale line = 1 mm.

tance as a percentage of trunk length, there do seem to be some species where this value remains reasonably constant over a wide range of sizes (e.g., *A. muelleri*, 95–100%). However, other species exhibit more variation (see Table 2 for *A. elegans*, 65–85% and *A. steenstrupii*, 70–90%). This is not clearly correlated with size. Therefore, while this attribute can be useful for differentiating two subsets, it does not have value at the species level.

The second aspect of this complex that is sometimes noted is the degree of fusion between these two muscles. In the older literature there is considerable confusion on this matter, such that some descriptions allege there to be only one or as many as four, or one muscle with one, two or four “roots.” From what we know about the ontogeny of this functional complex in sipunculans, it is probable that they all begin life with two pairs of retractors (Rice 1976). The dorsal pair is lost and the ventral pair fuses to vary-

ing degrees. However, quantifying this is extremely difficult because extension of the introvert will stretch out the muscle and the point of fusion will move away from the posterior end of the trunk. While one gets the impression that there are different sized muscles and different degrees of fusion, no pattern can be discerned. We are unable to suggest how this information can be universally applied even if species specificity was evident.

5. *Spindle muscle attachment.* — This thin muscle extends from the body wall at the posterior end of the trunk, through the gut coils, and along the rectum to the body wall just anterior to the anus. While there have been a few reports of this muscle merging with the body wall posterior to the anus, the only cases of this kind we have been able to confirm are in *A. laevis* and *A. coyi* in which the muscle sends a large branch to the mid-dorsal body wall posterior to the anus. It is not always easy to trace the course

Table 2.—Selected morphological attributes of *A. elegans* and *A. steenstrupii*.

<i>Aspidosiphon elegans</i>				<i>Aspidosiphon steenstrupii</i>			
Trunk length in mm	Retractor origin; % trunk	Nephridia length; % trunk	Nephridia attachment; % nephridium	Trunk length in mm	Retractor origin; % trunk	Nephridia length; % trunk	Nephridia attachment; % nephridium
6	83	75	89	7	71	42	67
7	86	70	95	7	79	57	75
7	—	57	95	10	75	50	50
8	63	63	99	11	82	45	75
9	67	50	99	11	73	99	67
10	70	60	67	12	75	50	67
10	70	70	93	12	75	99	99
11	82	64	99	14	79	54	75
14	86	57	88	15	77	50	—
15	60	67	50	15	80	60	56
15	80	40	83	15	73	67	50
16	63	53	85	15	73	60	50
16	81	63	99	17	82	41	71
16	88	88	95	19	79	58	50
17	76	35	99	19	68	47	67
17	65	65	82	19	84	47	90
19	79	58	86	20	85	75	40
19	74	47	99	21	76	57	—
21	90	52	64	22	77	68	50
22	86	86	95	24	71	42	75
23	78	57	99	25	80	48	58
25	84	60	67	26	81	69	50
32	78	56	99	27	70	81	99
				28	75	65	99
				33	79	67	50
				33	85	52	53
				34	85	50	50
				50	76	70	33
				50	80	54	75

of this muscle, especially in smaller worms or where the spindle muscle seems to merge with the wing muscle. Except for the above species, the muscle originates anterior to the anus and, therefore, in this genus, it is of limited usefulness as a diagnostic character.

6. *Fixing muscle number*.—In most sipunculan taxa fine thread-like muscles anchor some part of the anterior intestine to the body wall. The maximum number recorded in this genus is one and its presence (or absence) has been considered systematically important by some biologists. Our review of the literature reveals a lack of consistency on this point. Our own studies strongly suggest that either: A. Genetic poly-

morphism exists within populations or B. This fragile structure is placed where it can be easily damaged during dissection. While it may be true that some species totally lack this muscle and others usually have one, the possibility of any one worm deviating from the norm is too great to give weight to this character.

7. *Nephridia (length, attachment, level of nephridiopore)*.—Both the nephrostome and the nephridiopores are located at the anterior end of the nephridia, a pair of tubular sac-like ventro-lateral organs. These open to the outside at the anterior end of the trunk. Three attributes have been recorded and are sometimes treated as diagnostic.

First is the position of the nephridiopores relative to the anus. In the literature most species of *A. (Aspidosiphon)* and a few *A. (Paraspidosiphon)* are reported as having nephridia at the level of the anus but slightly posterior to it in the remaining species. In this latter group our own data show this distance to be 3–8% of the trunk length. However, even in these populations a few animals have the nephridiopores and anus at the same level. While there do seem to be other species where this distance is almost always zero, careful examination of more than ten worms will probably reveal one or two where these openings are not at the same level. It may be possible to say: “80–90% of species X have these openings at the same level while in species Y only 5–10% do.” But as these kinds of data are not always available (small sample sizes), the information has limited value to the systematist.

A second attribute is the length of these organs. The literature includes statements like “very long, long, reach to the base of the retractors, two-thirds/half/one fourth as long as the trunk,” etc. Our observations show a range of lengths within a population, not correlated with trunk size (see Table 2), but there are some differences among species. Six species have nephridia half the trunk length or less. Many exhibit a broad range (e.g., 25–100%, 45–85%, 50–100%) and a few have only long nephridia (over 85% of the trunk length). With a few exceptions, nephridia length can only be used in a limited manner.

A third attribute often mentioned is the attachment of the nephridia to the body wall by a membranous sheet of connective tissue. Occasionally this takes the form of filamentous strands of tissue scattered along the nephridia that bind them less tightly. While nephridial attachment often appears in keys to *Aspidosiphon*, its constancy is overrated. While the original description may state that the nephridia are attached for a particular length (one-half, two-thirds,

100%, etc.), subsequent authors either ignore it or do not verify it critically. The connective tissue is easily torn, and within a single worm the attachment can differ for each organ. In most species a wide range of values is observed, commonly in the 50–100% range (see Table 2 for *A. steenstrupii*, 50–80% and *A. elegans*, 80–100%) while *A. muelleri* ranges from 0–100% attached in different reports. Therefore, this attribute has restricted systematic value.

8. *Rectal caecum (presence, complexity)*.—In many sipunculans there is a small caecum on the rectum near the intestinal coil. Certain species of *Aspidosiphon* are reported to lack a caecum while others are said to have one. Two problems exist: If one looks at all of the published reports of any frequently recorded species, one finds inconsistencies, e.g., in *A. elegans* several authors say it lacks a caecum, others make no mention (this could mean that it is absent or possibly that they did not look for it), and a few report seeing the caecum. Alternatively, *A. muelleri* has been said to have a caecum by many authors but a few assert that it lacks one. In the *A. muelleri* we have recently examined, 25% have a caecum. In *A. albus* the original describer (Murina 1967c) asserts that the caecum is absent. Subsequent workers looking at other members of the population (Cutler 1973, Migotto & Ditadi 1988) saw one.

The second problem is related to this and it is illustrated by our finding a caecum in two of ten *A. elegans* we examined. Here we have one observer looking at one deme and finding dimorphism. In 30 worms that Migotto & Ditadi (1988) dissected they found a caecum in 18 (two of these being “large, villous”). In other words, 40% of this population of a species described as having a caecum was found to lack one. As this is true for one population, it may be true for all. We conclude that it is an error to consider the presence or absence of a rectal caecum as species specific.

In this genus there is one special case, i.e.,

a rectal structure described as: “. . . the last part of the rectum densely bordered with long villi-like structures” (Selenka et al. 1883 in *A. cumingii*) or “rectum with caecum plus many blind tubes attached to both sides” (Sato 1939 for *A. grandis*) or “rectum with a larger caecum, many lobed on both sides” (Selenka et al. 1883 in *A. klunzingeri*) or “rectal caecum with lappets” (Edmonds 1956 in *A. klunzingeri*) or “a large cluster of blind sacs as ramified intestinal appendages” (Wesenberg-Lund 1937 in *A. pachydermatus*). Only one specimen of *A. pachydermatus* and two of *A. grandis* (100, 70 and 100 mm trunks) exist. Of the 12 records of *A. klunzingeri* that include morphological comments, only the original material (3 worms) has this type of rectal elaboration. For subsequent authors, its absence seemed inconsequential. Similarly, in the nine reports of *A. cumingii* with morphological comments, only Selenka et al. (1883) record this structure in five worms (the words are used by other authors but only when referring to Selenka et al.). So, while these species supposedly have an elaborate rectum, several authors have used this name for animals lacking said structure. In museum collections, fewer than 10 worms exist (Baird's two have been lost) with this condition. The four worms in our 1985 Hawaii material that we are calling *A. laevis* have trunk lengths of 7, 10, 11 and 14 mm. The largest and the smallest bear a single structure with 6–8 short branches or lobes coming off each side. The 10 and 11 mm worms show small lobes, but the precise structure is less clear due to the fragility of the rectum. In our 1988 Venezuela collections we have five *A. laevis* (10–30 mm trunks), but none of these has a caecum of any kind. Migotto & Ditadi (1988) report large villous, simple and no caeca in a single population.

The question posed above reappears here: If an author did not mention this structure, does that mean it was not present? In those cases when an author specifically says that the complex caecum was not present, what

significance does that have? Historically the position that this is insignificant and variable within a population has implicitly prevailed. Our recent data confirm that and suggest that *A. laevis* has the genetic potential (perhaps polygenic), but this potential is not always expressed, and when it is expressed it may be overlooked by an observer.

9. *Intestinal coils (tightness)*.—In some other genera the number of gut coils has been used as a systematic character, but we have elsewhere shown this to be size dependent and not useful. In *Aspidosiphon* the interest is restricted to the nature of the coiling. In most species a regular, compact double helix is present, but *A. misakiensis* exhibits a loose, less regular helix (Fig. 4). This has also been reported by a few authors for *A. elegans*. The helix is maintained by the fine strands of muscle linking the coils to the axial spindle muscle. In those animals having a looser gut coil the linkage is not continuous and the strands may be longer.

10. *Longitudinal muscle (bundles, anastomosing, fracturing)*.—The body wall of sipunculans has an internal layer of longitudinal muscle. In one subgenus (*A. Aspidosiphon*) this is an undivided sheet, almost. In the other subgenus (*A. Paraspidosiphon*) this layer is divided into separate bundles. However, it is not always a clear-cut dichotomy. Intermediate conditions of two general types exist.

First, ten putative species of *A. (Aspidosiphon)* have been described as having fracturing of the muscle layer in the anterior dorsal trunk. Commonly this is restricted to the area under the anal shield, but in some species the fractures continue out beyond these borders for a small (10–20% of the trunk length) but variable distance.

The second variation occurs in species of *A. (Paraspidosiphon)* where the longitudinal muscle bands are not distinct. The degree of variation is much greater than in other genera with these bundles. While several have distinct rarely anastomosing bundles,



Fig. 4. Intestinal coil of *A. misakiensis* showing irregular loose arrangement (A—anal shield, M—retractor muscle, N—nephridium, R—rectum). Scale line = 2 mm.

many exhibit a modest degree of anastomosing and others show frequent cross linkages. In these latter the layer appears like a continuous sheet that has split or fractured and not like distinct bundles (e.g., *A. fischeri*).

The number of muscle bands varies considerably within a population and within an individual (25–35 anteriorly and 15–25 posteriorly). It is difficult in a few cases, especially in small worms, to know whether one is looking at an *A. (Paraspidosiphon)* with much anastomosing of bundles or at an *A. (Aspidosiphon)* with some fracturing of a layer.

While this character state may be used for separating subgenera, it is neither species

specific nor discriminating at that level. Since the subdivision of a continuous layer appears to be an homoplastic, apomorphic condition (Cutler & Gibbs 1985) it is possible that it has arisen more than once within this genus. Therefore, using it as the single attribute to separate subgenera may mask actual phylogenetic relationships.

11. *Angle of introvert to trunk.*—In most *Aspidosiphon* the extended introvert protrudes at an angle of 75–90° to the main axis of the trunk at the ventral edge of the anal shield. However, in at least three species, all with very weakly developed anal shields, this angle is reduced to 45–60°. While this is not broadly useful, it can help in these special cases.

Summary.—Two characters that have broad taxonomic usefulness are the hook and anal shield morphology. Four characters useful for separating the genus into different subsets are: (1) longitudinal muscle layer continuous or divided, (2) retractors originating in the most posterior 5% of the trunk or in the 70–80% range, (3) caudal shield developed or not, and (4) nephridia length (less than 50% of trunk length, more than 75%, or a broad range). An introvert/trunk angle of less than 75° separates three species, while a bifurcated anterior spindle muscle and a loosely wound gut coil each characterizes one species. The presence/absence of fixing muscles or caecum, the placement of the nephridiopores, and the attachment of the nephridia to the body wall are too variable to have any systematic value in this genus.

Systematic Section

Aspidosiphon Diesing, 1851

Diagnosis.—Introvert usually longer than trunk. Recurved hooks in numerous rings (absent in three, only scattered in two species). Trunk with anal shield composed of hardened units (occasionally inconspicuously developed). Introvert protrudes from ventral margin of shield. Body wall either with continuous longitudinal muscle layer or with longitudinal muscle layer gathered into anastomosing, sometimes ill-defined, bundles. Oral disk with tentacles enclosing dorsal nuchal organ but not mouth. Contractile vessel without villi. Two introvert retractor muscles sometimes almost completely fused. Spindle muscle attached posteriorly. Two nephridia. One species may exceed 100 mm but most less than 40 mm long.

We herein create a new subgenus for a set of five species as defined below. The major character state we focus on is the absence of compressed hooks in rings, a plesiomorphic character state for this entire class (Cutler & Gibbs 1985). One could argue that

these species represent primitive transition forms from a very early ancestral stock, but we propose instead that this trait has been secondarily lost through subsequent evolution, i.e., a type of reversal. In support of this, note the atypical ecology of these taxa (e.g., interstitial or abyssal, none boring in coral or rock) suggesting an ecological specialization.

The following four taxa are not considered valid members of this genus and are discussed first. After the key, the remaining species are presented alphabetically within subgenera.

Aspidosiphon cylindricus Horst, 1899

Aspidosiphon cylindricus Horst, 1899:195–198, text-figs. 3–4.—Stephen & Edmonds, 1972:222–223.—Not Sluiter, 1902:18–19.

Material examined.—ZMUA, Sluiter's material (V. Si. 26.8).

Discussion.—This species was based on a single worm that disappeared from the Leiden museum prior to 1930 (van der Lund, pers. comm.). Enough questionable but now unverifiable features exist (especially the hook morphology) that we place this name on the list of *species inquirenda* pending future clarification. Sluiter's (1902) material was reexamined and is herein referred to *A. elegans*.

Aspidosiphon insularis (Lanchester, 1905)

Aspidosiphon insularis Lanchester, 1905b: 40, pl. 2, fig. 4.—Gibbs & Cutler, 1987: 56.

Paraspidosiphon insularis.—Stephen & Edmonds, 1972:247.

Material examined.—BMNH, type (1924.3.1.80).

Discussion.—This worm is in poor condition, but, as noted by Gibbs & Cutler (1987), it is clearly a *Phascolosoma* and based on hooks and papillae is a junior synonym of *P. perlucens*.

Aspidosiphon macer (Sluiter, 1891)

Phascolosoma macer Sluiter, 1891:114–115, pl. 2, figs. 13–14; 1902:34.

Golfingia macra.—Stephen & Edmonds, 1972:149.—Cutler & Murina, 1977:183.

Aspidosiphon macer.—Cutler & Cutler, 1986:568.

Material examined.—ZMUA, type and only specimen (V. Si. 65).

Discussion.—This putative taxon is based on a single specimen that has been thoroughly dissected over the years. The generic status is not altogether firm since the anal shield is very poorly developed and the introvert does not appear to be ventrally displaced. The gut is missing and while Sluiter asserted that the spindle muscle is not attached posteriorly, there is a muscle coming from the center of the caudal shield that we interpret as the broken posterior portion of this muscle. Sluiter said there were no hooks but there are about ten distinct rings of sharply pointed, unidentate hooks. The longitudinal muscle layer is undivided. While Sluiter asserted that the tentacles surround the mouth, the introvert is not extended so one cannot really tell how the tentacles are arranged. They appear to us to be clustered towards one side as in this genus. Therefore, until additional material is obtained to clarify this uncertainty, we place this name on the list of *species inquirenda*.

Golfingia mokyevskii Murina, 1964

Golfingia mokyevskii Murina, 1964a:256–259, figs. 4–5.

?*Aspidosiphon mokyevskii*.—Gibbs et al., 1983:302.

Material examined.—ZIAS, type material.

Discussion.—Gibbs et al. (1983) suggested that Murina's species might be an *Aspidosiphon*; however, it is now clear that this was an error. The 50 long tentacles, absence of hooks, anastomosing longitudinal muscle bands, large dark papillae at the base of the

introvert, and especially the presence of contractile vessel villi all support placing this name in the synonymy of *Antillesoma antillarum*.

Key to *Aspidosiphon* species

1. Hooks not present, or if present, not in rings *A. (Akrikos)* 2
- Hooks arranged in rings on distal portion of introvert 6
2. Introvert hooks absent 3
- Scattered introvert hooks present 5
3. Anal shield of tightly packed, uniform sized, pale, flat units with distinct angular margin *A. albus* Murina
- Anal shield of dispersed, often dark units, sometimes very poorly developed, with indistinct margin . . 4
4. Anal shield units distinct, dark; those around margin usually pointed cones
- . . . *A. venabulum* Selenka, de Man & Bülow
- Anal shield units indistinct, widely spaced, flat, sometimes arranged in indistinct rows
- *A. thomassini* Cutler & Cutler
5. Anal shield ill defined and diffuse, trunk usually more than 5 mm, shallow warm water
- *A. mexicanus* Murina
- Anal shield well defined and compact, trunk usually less than 5 mm, deep cold water *A. zinni* Cutler
6. Longitudinal muscles in continuous layer (except under anal shield) *A. (Aspidosiphon)* 7
- Longitudinal muscle layer divided into separate (or anastomosing) bundles . . *A. (Paraspidosiphon)* . . 13
7. Anal shield with extensive array of furrows present, not just around margin 8
- Anal shield with randomly distributed hardened units, lacking extensive grooves/furrows 9

- 8. Individual units form into longitudinal ridges over dorsal half of anal shield *A. muelleri* Diesing
- Individual units arranged in offset squares or rectangles *A. spiralis* Sluiter
- 9. All hooks unidentate, ill-defined anal shield *A. gracilis* (Baird)
- Distal hooks bidentate, anal shield distinct 10
- 10. All compressed hooks bidentate followed by dark conical hooks *A. elegans* Chamisso & Eysenhardt
- Distal bidentate compressed hooks followed by proximal unidentate ones 11
- 11. Interstitial, introvert 2–5 times the trunk length, nephridia 25–33% trunk *A. exiguus* Edmonds
- Occupies coral or shells often subtidal, introvert 1–3 times trunk, nephridia more than 50% of trunk length 12
- 12. Normal gut helix, lives in gastropod shells, anal shield units square, arranged in rows, and each made up of smaller granular subunits *A. gosnoldi* Cutler
- Gut coils loose or absent, does not occupy gastropod shells, anal shield units more solid and randomly arranged *A. misakiensis* Ikeda
- 13. Anal shield ungrooved or, if present, only as short marginal ones (Fig. 5A) 14
- Anal shield with extensive grooves or furrows present (Fig. 5B) 18
- 14. Distal hooks bidentate 15
- All hooks unidentate *A. planoscutatus* Murina
- 15. Compressed hooks bidentate followed by dark pyramidal hooks *A. steenstrupii* Diesing
- Compressed hooks of both types, pyramidal hooks pale, if present 16
- 16. No pyramidal hooks, longitudinal muscle bands distinct, compressed hooks over 30 μm tall, retractor origins 75–88% *A. tenuis* Sluiter
- Pale pyramidal hooks present, longitudinal muscle bands indistinct, hooks less than 30 μm tall, retractor origins 95–100% 17
- 17. Anal shield marginally becomes diffuse forming cones or spikes, nephridia more than 1/2 trunk *A. parvulus* Gerould
- Anal shield with distinct margins, no cones or spikes, nephridia less than 1/2 trunk *A. fischeri* ten Broecke
- 18. All hooks unidentate, retractor origins not at posterior end (60–80%) *A. laevis* Quatrefages
- Distal hooks usually have very small secondary tooth, retractor origins at posterior end (95–100%) *A. coyi* Quatrefages

Aspidosiphon (*Akrikos*), new subgenus

Diagnosis. — *Aspidosiphon* with compressed hooks not in rings, i.e., either scattered and small (less than 30 μm), or absent; caudal shield absent or very diffuse; longitudinal muscle layer continuous. Not known to bore in coral or rock.

The name is from the Greek meaning “without rings.” The spelling is a literal transliteration according to the classical method.

Type species: *Aspidosiphon albus* Murina, 1967.

Aspidosiphon albus Murina, 1967

Aspidosiphon albus Murina, 1967a:1330–1331, fig. 2 (1)–(3).—Stephen & Edmonds, 1972:219–221.—Cutler, 1973:174–175.—Cutler & Cutler, 1980a:4.—Migotto & Ditadi, 1988:247–248.—Not Cutler et al., 1984:307.

Aspidosiphon hartmeyeri. —Wesenberg-Lund, 1957a:7–8; 1959a:197; 1959b:212.

Material examined. —ZIAS, type; USNM, cataloged as *A. cumingii* 066214-222 off Louisiana; material from Brazil (Cutler &

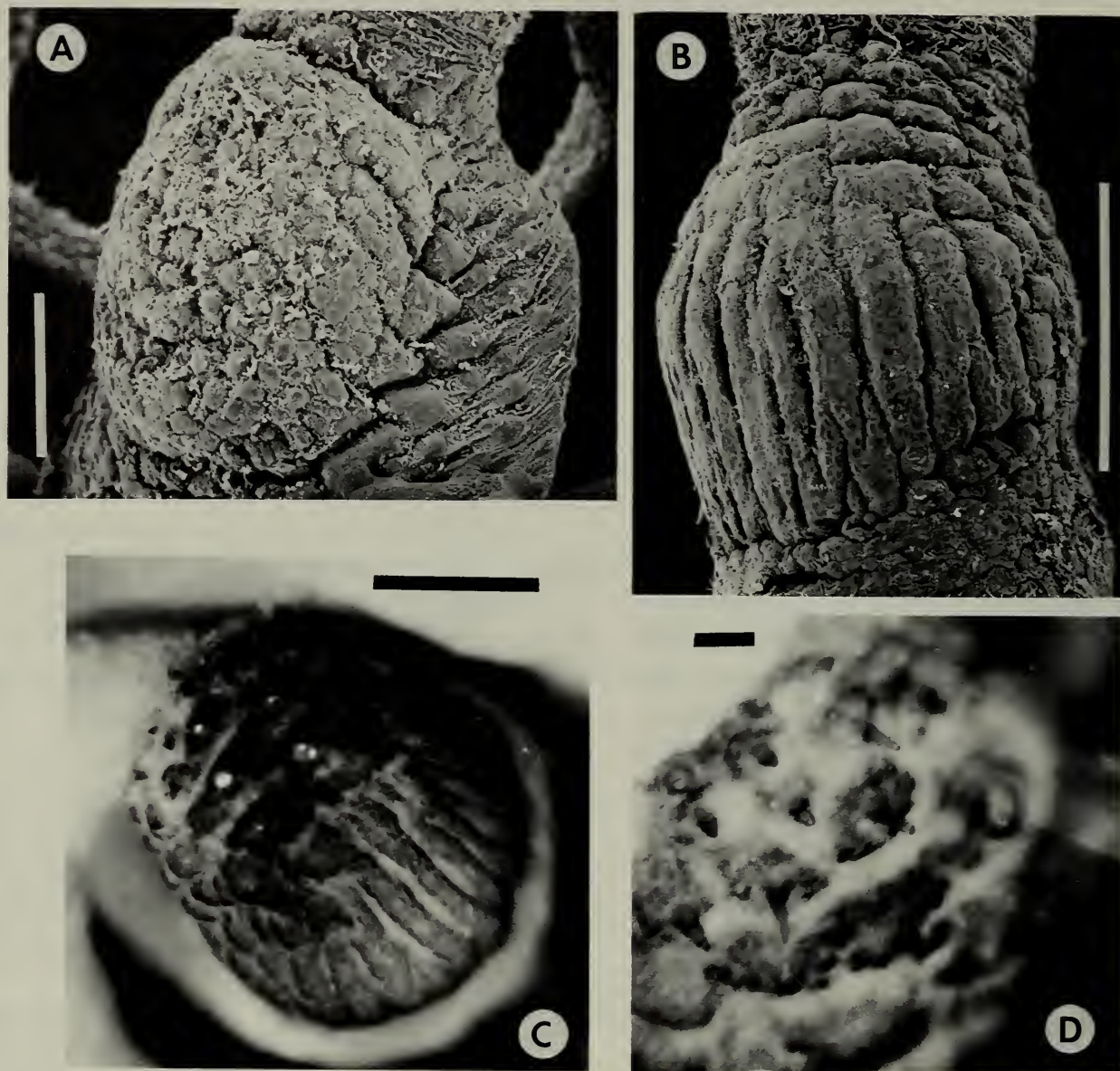


Fig. 5. Anal shields: A, Ungrooved type of *A. elegans*; B–C, Grooved type as in *A. muelleri*; D, Ventral cone-shaped units near the ventral margin present in some *A. muelleri*. Scale lines on A, B, C = 0.5 mm, D = 0.1 mm.

Cutler 1980a), U.S. east coast (Cutler 1973), and new Ivory Coast material from 5°N, 4°W, at 20 m; *A. hartmeyer*, UZMK, Wesenberg-Lund's Niger worms.

Discussion.—This hookless species also seems to lack tentacles. The recorded body length ranges from 2 to 45 mm, the introvert is 3–5 times the trunk length, and the anal shield is fine grained with small furrows around the margin but without grooves. Often there is a median stripe made up of darker units. The nephridia are 50–75% of the trunk.

The Cutler et al. (1984) record was based

on one incomplete worm and was not a positive identification. This should not be included within this species unless additional material is found in Japanese waters.

Distribution.—Cape Hatteras, northern Gulf of Mexico (unpublished), Cuba, Brazil continental shelf (10–123 m), and the east Atlantic from the Gulf of Guinea. It is the most common member of this genus on the Brazilian shelf.

Aspidosiphon mexicanus (Murina, 1967)

Golfingia mexicana Murina, 1967c:1333–1334, fig. 3.

Aspidosiphon mexicana Cutler et al., 1983: 673.

Aspidosiphon longirhyncus Cutler & Cutler, 1980a:4–6, figs. 4–5.

Material examined.—ZIAS, type; *A. longirhyncus*, AMNH, type (4022); other material of both species from the type localities. Also, 12 unpublished specimens from the Azores (33°N, 16°W, 320 m) and seven from three stations off Florida and North Carolina (25–34°N, 85–190 m).

Discussion.—This species does not have the typical aspidosiphonid appearance in that the anal shield is very weakly developed with scattered, ill-defined platelets. Also, the introvert is on an atypical angle (45–60°) with the main trunk axis. The caudal shield is almost nonexistent. The introvert is 4–5 times the trunk length, bearing scattered, small (less than 30 μm), unidentate compressed hooks. The nephridia are 35–75% of the trunk.

The decision to combine these two names was discussed in Cutler et al. (1983) as part of a review of the taxon containing Murina's species.

Distribution.—Southern Brazil, Cuba, and southeastern U.S. at shelf depths (80–200 m), and the Azores at 320 m.

Aspidosiphon thomassini
Cutler & Cutler, 1979

Aspidosiphon thomassini Cutler & Cutler, 1979a:971–973, figs. 3–14.

Material examined.—MNHN, type material (AH 406–408).

Discussion.—This is another small (1.5–7 mm) hookless species whose tentacles (if present) have yet to be observed. The retractor muscles are fused for most of their length and the nephridia are around 50% of the trunk. The introvert is 2–4 times the trunk length. These have no caudal shield and the anal shield is very poorly developed. This, together with the smaller angle between the trunk and introvert axis (40–45°) make it possible to mistakenly identify this as a *Nephasoma* species.

Distribution.—Intertidal coral sands in Madagascar and French Polynesia.

Aspidosiphon venabulum
Selenka, de Man & Bülow, 1883

Aspidosiphon venabulum Selenka et al., 1883:123, pl. 14, figs. 202–204.—Fischer, 1895:18; 1914a:68–69.—Wesenberg-Lund, 1957c:5–7; 1959a:196–197; 1959c:212.—Longhurst, 1958:85.—Stephen, 1960a:519.—Cutler, 1977a:148.

Aspidosiphon venabulus.—Stephen & Edmonds, 1972:237.—Cutler & Cutler, 1979a:971.

Material examined.—MNHU, type (644); UZMK, Wesenberg-Lund's Atlantide material; worms from Madagascar (Cutler & Cutler 1979a) and West Africa (Cutler 1977a).

Discussion.—This species lacks hooks and the anal shield is ungrooved, being made up of dark, pointed, conical units more widely scattered than in many species. It resembles the anterior end of certain *Phascolion* species that have large anterior papillae. The retractor muscles extend to the posterior end and under the anal shield, the longitudinal muscle layer splits into a few bundles. The nephridia are 60–95% of the trunk, the latter being reported from 5–30 mm.

Distribution.—Subtidal depths (10–55 m with one intertidal report and one at 960 m). Most records are off West Africa with one report from southern Madagascar.

Aspidosiphon zinni Cutler, 1969

Aspidosiphon zinni Cutler, 1969:209–211, fig. 1.—Cutler, 1973:176–178.—Cutler & Cutler, 1979a:968; 1980b:457; 1987a:73.

Material examined.—USNM, type material (38242, 38243); Atlantic Ocean material (Cutler & Cutler 1987a).

Distribution.—This small (most less than 5 mm), deep-water worm commonly lives in foraminiferan tubes. The anal shield is made up of very fine grained, pale units and the caudal shield is nonexistent. The small

(15–20 μm), scattered, unidentate, compressed hooks and introvert not longer than the trunk are unusual in this genus. The nephridia are less than 25% of the trunk.

Distribution.—Common in north Atlantic Ocean (1100–4400 m), two stations around 9°S off the Congo River (1535 and 2700 m), and one in the Mozambique Channel (25°S) at 132 m.

Subgenus *Aspidosiphon* (*Aspidosiphon*)

Diagnosis.—Introvert with compressed hooks in rings, longitudinal muscle layer continuous except near anal shield. Most do not bore in coral or rock.

Aspidosiphon elegans

(Chamisso & Eysenhardt, 1821)

Sternaspis elegans Chamisso & Eysenhardt, 1821:351–352, pl. 24, figs. 5a–e.

Sipunculus elegans.—de Blainville, 1827, pl. 26, fig. 2.

Loxosiphon elegans.—Diesing, 1851:70.—Quatrefages, 1865:605.

Phascolosoma (Aspidosiphon) elegans.—Grübe, 1868a:645–647.

Aspidosiphon elegans.—Selenka et al., 1883:124–126.—Shipley, 1898:471; 1899b:153.—Whitelegge, 1899:393.—Sluiter, 1891:116; 1902:19.—Hérubel, 1904:564.—Lanchester, 1905a:33; 1905b:40.—Fischer, 1914b:14.—Gravelly, 1927:87.—Sato, 1935:316; 1939:426–427.—Wesenberg-Lung, 1954:10–11; 1957a:198–199; 1957b:7–8; 1959c:68.—Cutler, 1977b:154.—Cutler & Cutler, 1979a:968.—Edmonds, 1980:44–46.—Cutler et al., 1984:304.—Migotto & Ditadi, 1988:248–250.

Aspidosiphon elegans elegans.—Stephen & Edmonds, 1972:223.

Aspidosiphon elegans var. *yapense* Sato, 1935:316–318, pl. 4, fig. 18, text-figs. 12–15.

Aspidosiphon elegans yapensis.—Stephen & Edmonds, 1972:224.

Aspidosiphon brocki Augener, 1903:328–

330, figs. 9–13.—Murina, 1967b:42.—Rice, 1970:1618–1620; 1975:44–45.—Stephen & Edmonds, 1972:221.—Rice & Macintyre, 1979:311–319.

Aspidosiphon carolinus Sato, 1935:318–319, pl. 4, fig. 19, text-figs. 16–17.—Stephens & Edmonds, 1972:222.—Cutler & Cutler, 1981:77–78.

Aspidosiphon cylindricus.—Sluiter, 1902:18–19.

Aspidosiphon exilis Sluiter, 1886:497, pl. 3, figs. 11–12; 1891:116; 1902:18.—Leroy, 1942:39–40.—Stephen & Edmonds, 1972:224–225.—Edmonds, 1980:44–46.

Aspidosiphon homomyarium Johnson, 1964:332–334, pl. 8.

Aspidosiphon homomyarius.—Stephen & Edmonds, 1972:227.

Aspidosiphon ravus Sluiter, 1886:495–496, pl. 3, figs. 9–10; 1891:116; 1902:18.—Shipley, 1899a:56; 1899b:153.—Stephen & Edmonds, 1972:234.

Aspidosiphon spinalis Ikeda, 1904:47–49, text-figs. 12, 81–85; 1924:37.—Sato, 1939:428.—Stephen & Edmonds, 1972:234–235.—Cutler & Cutler, 1981:79–81.

Aspidosiphon spinosus Sluiter, 1902:28, pl. 2, figs. 17–19.—Stephen & Edmonds, 1972:235.

Material examined.—ZMUA, Sluiter's from Indonesia (V. Si. 3); worms from the western Pacific Ocean (Cutler et al. 1984), 1988 collections from the southern Caribbean, a few from Brazil (Migotto & Ditadi 1988); *A. brocki*, MNHU, type material (6954-5); USNM, Caribbean material identified by M. Rice (USNM 48924-5); *A. cylindricus*, ZMUA, two of Sluiter's (26.8); *A. exilis*, BMNH and ZMUA (V. Si. 4), parts of type material in both places, all of it badly dried out; *A. homomyarius*, RSME, two worms from India presumably deposited by Johnson (1965.32.1); *A. ravus*, ZMUA (V. Si. 13) and BMNH, type material.

Discussion.—Like *A. (Paraspidosiphon) steenstrupii* in its subgenus, *A. elegans* is the most common and widespread tropical

member of this subgenus with many junior synonyms. Additionally, both species have ungrooved anal shields, bidentate compressed hooks in rings, and dark scattered hooks. Edmonds (1980:44–45) presented a detailed description of *A. elegans* and some interesting comments on this complex of related (or identical) taxa. What he illustrates as introvert spines (his figs. 77–78) are, by our definition, conical hooks. The variation in the shape (real and due to orientation on slide) of the bidentate hooks has led to the creation of different species. Figure 6 illustrates some of this variation (degree the hook is bent and sharpness of the point) that we now know to be within-deme variation. Six to twelve short stubby nuchal tentacles are present. The caudal shield is weakly developed, barely discernable in many worms.

Internally the longitudinal muscle layer may subdivide in the area of the anal shield. Less than 20% of the worms dissected have a caecum and a fixing muscle was seen in only 4% of the worms dissected. The nephridia open at the level of the anus or just posterior to it. Table 2 shows our observations on the nephridia and retractor origins. The gut has the normal helical coil, but about half the worms show a degree of looseness in part of the coil.

The putative species *A. carolinus* and *A. spinalis* were reduced to junior synonyms by Cutler & Cutler (1981) and *A. exilis* by Edmonds (1980). We reaffirm those decisions.

Aspidosiphon brocki (Augener 1903) is a name used by only two authors since it was described: Murina (1967b) and Rice (1970, 1975). Neither of these authors has used the name *A. elegans* in their writings. Augener's paper was the first of only two articles he wrote about this phylum, and he made no reference to any other member of this subgenus nor was there a differential diagnosis. The original report was from Malaya but the four subsequent records are all Caribbean, and all of this latter material is less



Fig. 6. Variation in shape of bidentate compressed hooks within a single specimen of *A. elegans*. Note difference in degree of bend and sharpness of point. Scale line = 20 μm .

than 10 mm long. Our recent Caribbean collections (340 worms) ranged from 4 to 22 mm long. The pictures of hooks in Stephen & Edmonds (1972:230, fig. 27B, F, G) illustrate the extremes of a continuum and could be misleading. This much variation occurs within demes. Comparison of the type, Rice's material, and our own Caribbean and Pacific material convinces us that this putative species is conspecific with *A. elegans*.

Rice (1970) reported asexual reproduction by budding in *A. brocki*, something not recorded elsewhere in this phylum. Our Caribbean material showed this (even in 4 mm worms), but it is also present in our collections from Majuro, Marshall Islands, and in French Polynesian worms collected by Peyrot-Clausade.

Sluiter's (1902) *Siboga* report included *A. cylindricus*, Horst, but not *A. elegans*. Our examination of his material showed no differences from *A. elegans*.

When Johnson (1964) described *A. homomyarius*, he did not include a differential diagnosis except to contrast it with the other new species in that paper, so we do not know how he thought it differed from *A. elegans*.

He seemed to think that the dorsal array of nuchal tentacles was unique in this genus. Our examination of his two worms in Edinburgh confirmed our analysis of his article, i.e., meaningful differences from *A. elegans* are lacking.

Aspidosiphon ravus was described by Sluiter (1886) as having unidentate hooks. Our reexamination of the material (the Amsterdam worms are in good condition but the London worm is not) revealed bidentate compressed and conical hooks. The introvert is retracted in all three worms. This material is clearly conspecific.

Aspidosiphon spinosus Sluiter, 1902, was based on a single worm that has subsequently been lost. His description is indistinguishable from *A. elegans*. He compared it to *A. exilis* differentiating it by the form of the hooks and a few other features. Placing this name on the list of *incertae sedis* was considered since it cannot be examined (the hypothesis cannot be tested) but reducing it to a junior synonym of this species is a rational alternative given what we now know about within-deme variation.

The subspecies *A. elegans yapensis*, which Sato (1935) described as a variety, was differentiated on the basis of hook morphology: sharply pointed apex, not blunt. The within-deme variation we find makes it clear that this subspecies lacks biological significance.

Distribution.—Widespread and common in the Indian and western Pacific Ocean (from southern Japan to northern Australia out to Hawaii); the Red Sea and Israel. In the Caribbean from northern Brazil to the Florida keys and Bermuda.

Aspidosiphon exiguus Edmonds, 1974

Aspidosiphon exiguus Edmonds, 1974:187–192, figs. 1–7.

Material examined.—BMNH, holotype (1975.22.1).

Discussion.—The largest worm reported is less than 4.5 mm long, but it does bear bidentate hooks in rings as well as a few

scattered unidentate compressed hooks. The introvert is very long (2–5 times the trunk) and no tentacles or gametes have yet been observed. The anal shield consists of small, pale units with no grooves. At the anterior/ventral border 1–4 cone-like papillae are present. It is similar to *A. albus* but has hooks and shorter nephridia (25–33%). In the anterior 10% of the trunk the longitudinal muscle layer is divided into bands visible through the body wall. *Aspidosiphon (Paraspidosiphon) parvulus* is common in this area and is similar in several ways despite having longitudinal muscle bands (weakly developed).

Distribution.—Cuba, intertidal, interstitial.

Aspidosiphon gosnoldi Cutler, 1981

Aspidosiphon gosnoldi Cutler, 1981:445–449, figs. 1–4.—Migotto & Ditadi, 1988:253–254.

Aspidosiphon spinalis.—Cutler, 1973:175–176.—Cutler & Cutler, 1979b:107.

Material examined.—USNM, type (61624-5) and additional material from the western Atlantic Ocean (Cutler 1981).

Discussion.—The anal shield is composed of randomly arranged flat units of relatively uniform size. The borders are usually distinct but dark skin papillae may be present at the anterior end of the trunk. The introvert is 1.5–3 times the trunk length and bears distal rings of 20–30 μm , bidentate hooks (the secondary tooth may be small). Scattered, pale, pyramidal hooks cover much of the proximal part of the introvert. This is in the group of species where the longitudinal musculature commonly splits into irregular bundles under the anal shield and the retractors originate from the caudal shield. The intestine forms a normal helical coil, and the nephridia are 50–90% of the trunk length.

Distribution.—Shelf waters (7–185 m) from Cape Hatteras to Florida and Brazil (to 23°S) living in gastropod shells.

Aspidosiphon gracilis gracilis
(Baird, 1868)

Pseudoaspidosiphon gracile Baird, 1868:103,
pl. 10, figs. 1, 1a.

Aspidosiphon gracilis—Selenka et al., 1883:
122–123.—Sluiter, 1902:17.—Augener,
1903:319–321.—Hérubel, 1904:564.—
Rice & Stephen, 1970:69.—Stephen &
Edmonds, 1972:225–226.—Gibbs, 1978:
85.—Edmonds, 1980:46–47.

Material examined.—BMNH, syntypes
(43.5.15.58a/b); MNHN, two of Hérubel's
specimens (V20).

Discussion.—This species has an under-
developed anal shield composed of non-
contiguous brown papillae surrounded by
darker platelets. These units are arranged in
irregular longitudinal rows. The introvert
comes off at about a 60° angle, is up to 1.5
times the trunk length, and the slender trunk
(up to 15 times the width) is coarsely pap-
illated all over. The assertion that bidentate
hooks are present (Stephen & Edmonds
1972) must be a flawed translation since we
cannot find any other reference to them. The
unidentate hooks are in rings, are broader
than high (up to 40 μm), and are followed
by a proximal area of pyramidal hooks. The
retractor muscles originate very near the
posterior end and the nephridia are as long
as the trunk.

Hérubel (1904) had three worms from the
Gulf of Aden that look different but are
damaged and desiccated such that we can-
not confirm or refute his identification.

Distribution.—Australia, Indonesia, Phil-
ippines, Gulf of Aden and an unpublished
record from the Andaman Islands.

Aspidosiphon gracilis schnehageni
Fischer, 1913, new status

Aspidosiphon schnehageni Fischer, 1913:99–
100, figs. 4–6; 1914b:15.—Wesenberg-
Lund, 1955:13.—Ditadi, 1975:200–202.

Paraspidosiphon schnehageni.—Stephen &
Edmonds, 1972:252.

Material examined.—ZMUH, type spec-
imen (V2127).

Discussion.—The type specimen is in very
poor condition, missing, among other parts,
the distal end of the introvert and the re-
tractor muscles. Ditadi (1975) redescribed
this taxon, but his material cannot be lo-
cated at the Los Angeles County Museum
or the Hancock Foundation where it had
been deposited. The anal shield was de-
scribed as furrowed by Fischer but as ran-
domly arranged plates by Ditadi. This is
another situation where the units may
sometimes appear arranged in rows giving
an impression of indistinct ridges and fur-
rows. The longitudinal musculature is par-
tially separated into 10–14 anastomosing
bundles in the anterior part but is contin-
uous elsewhere. In this regard, it is one of
the borderline taxa not having distinct bun-
dles, and, therefore, we have moved it into
this subgenus.

The decision to reduce this to a subspecies
rather than a junior synonym was based on
ill-defined differences from the nominate
form; habitat (mollusc shells), hook shape
(more triangular), nephridia (shorter, 33–
50%), trunk size and shape (length less than
8 times the width), and longitudinal muscle
layer (splitting extends beyond the anal
shield). These are not clear or distinct dif-
ferences by themselves, but if one adds the
geographical gap between the populations
(most of the Pacific Ocean), this status may
be appropriate pending additional material
for better comparison. The west coast of
Central and South America are very poorly
represented in curated, accessible collec-
tions.

Distribution.—Chile and Pacific coast of
Guatemala.

Aspidosiphon misakiensis Ikeda, 1904

Aspidosiphon misakiensis Ikeda, 1904:41–
43, text-figs. 9, 68–72.—Sato, 1939:428.—
Stephen & Edmonds, 1972:229–231.—
Cutler & Cutler, 1981:78–79.—Cutler et
al., 1984:305–306.

Aspidosiphon hartmeyeri Fischer, 1919:281–282, text-figs. 1–3; 1926:204–205.—Edmonds, 1956:306–307; 1980:47.—Murina, 1967c:1332.—Stephen & Edmonds, 1972:226–227.—Cutler, 1977a:147–148. Not Wesenberg-Lund, 1957a:7–8; 1959a:197; 1959b:212.

Aspidosiphon gerouldi ten Broeke, 1925:93, text-figs. 23–25.—Stephen & Edmonds, 1972:225.—Cutler & Cutler, 1979b:106–107.—Migotto & Ditadi, 1988:251–253.

Aspidosiphon speculator.—Saiz Salinas, 1986a:11–14.

Material examined.—USNM, paraneotype; other material from the type locality (Cutler & Cutler 1981); *A. gerouldi*, ZMUA, type (V. Si. 7), material from Azores (Cutler & Cutler 1987), and Brazil (Migotto & Ditadi 1988); *A. hartmeyeri*, ZMUH (V8913–14) and MNHU (6036), co-types; UZMK, Wesenberg-Lund's Niger material (= *A. albus*); *A. speculator*, three specimens identified by Saiz Salinas.

Discussion.—The anal shield is composed of closely packed, irregular, granular units, but it has borders that are not sharply defined, i.e., widely spaced, square blocks of shield material are around the anterior quarter of the trunk. The caudal shield is granular but does have vague radial grooves present. Bidentate hooks are present (25–40 μm) in distal rings, then proximally the hooks are scattered, unidentate compressed, 25–60 μm tall (Fig. 1B). The secondary tooth has normal dimensions on distal hooks but becomes very small in proximal ones. The introvert is up to three times the trunk length (largest known worm is 25 mm). The longitudinal muscle layer exhibits some fractures/splits in some individuals, and the gut coils are ill defined or only loosely wound. In 6–7 mm worms the intestine has a few loose folds, is anchored at the posterior end, then has a straight tube to the anus. Sheets of connective tissue link the ascending and descend-

ing loops. The nephridia are 50–100% of the trunk and the retractors originate very close to the caudal shield.

When Fischer (1919) described *A. hartmeyeri* from Australia, he made no reference to Ikeda's *A. misakiensis* even though it is clear he knew of Ikeda's paper. Stephen & Edmonds' (1972) key uses the nephridia being mostly free to separate it from Ikeda's. Our examination of five type specimens showed considerable variation (up to 80% attached and length up to 100% of the trunk, not 0% and 50% as stated). The anal shield was described as having 5–6 flat grooves. These are not grooves but irregular units arranged in indistinct rows in a few worms (see also Edmonds 1956:306). Wesenberg-Lund's four worms from West Africa are clearly part of the *A. albus* population. She never recorded hooks, and her drawings of one, plus our examination of another, confirm this.

The decision to reduce the status of *A. gerouldi* came after examination of unpublished material from the Azores and comparison to the Japanese worms. The original description was based on a single worm, but several hundred have been subsequently collected. The bidentate hooks in the Azores population are at the small end of the range (25–30 μm) as is the introvert (only up to twice the trunk in worms up to 20 mm long).

Saiz Salinas (1986a) used the name *A. speculator* for 18 worms off Spain and the Canary Islands. This population is particularly troublesome as indicated by his placing it in *A. (Paraspidosiphon)*. The longitudinal musculature is neither continuous nor divided into distinct bands. It varies from worm to worm in degree, but we interpret it to be continuous with fracturing in the anterior part, especially on the dorsal side. In other respects (hooks, shield, gut) his worms fit *A. misakiensis* better than any other taxon.

Distribution.—In the Pacific from both sides of central Japan at 1–50 m depth, South

and West Australia, and Kermadec Island. In the eastern Atlantic from the Azores, Cape Verde, and Canary Islands to the Gulf of Guinea, at depths down to 75 m, and the Spanish Mediterranean. In the western Atlantic from Brazil (14–16°N), Haiti, and Cuba.

Aspidosiphon muelleri Diesing, 1851

Aspidosiphon muelleri Diesing, 1851:68.—Quatrefages, 1865:609–610.—Schmidt, 1865:56–66.—Baird, 1868:101.—Selenka et al., 1883:120–121.—Fischer, 1895:18; 1914a:69–70; 1914b:13–14; 1922a:22–23; 1925:25–26.—Sluiter, 1900:14; 1902:18; 1912:19.—Hérubel, 1904:564.—Southern, 1912:31–34.—J. Fischer, 1914:105–106.—Ikeda, 1924:38.—Stephen, 1934:173; 1941:257; 1958:133–134; 1960a:518–519; 1960b:22–23.—Steuer, 1936:5; 1939:2.—Sato, 1939:428.—Chapman, 1955:351.—Wesenberg-Lund, 1957a:4–5; 1957b:197–198; 1959a:194–196; 1959c:68.—Longhurst, 1958:1.—Stephen & Edmonds, 1972:231–233.—Zavodnik & Murina, 1975:127; 1976:81–82.—Cutler, 1977a:148.—Gibbs, 1977:30–31.—Cutler & Cutler, 1979b:107; 1987a:73.—Ocharan, 1980:114–115.—Cutler et al., 1984:306–307.—Saiz Salinas, 1984:177–178; 1986a:9–11.

Sipunculus scutatus J. Müller, 1844:166–168 (not *scutatum* J. Müller, 1843).—Keferstein, 1867:52.—Selenka et al., 1883:120.

Phascolosoma scutatum.—Krohn, 1851:371.—Selenka et al., 1883:120.

Aspidosiphon clavatus.—Diesing, 1851:68.—Cuénot, 1922:12–13.—Hérubel, 1924:111.—Leroy, 1936:426.—Åkesson, 1958:206.—Voss-Foucart et al., 1977:135.

Pseudaspidosiphon clavatum.—Baird, 1868:103.

Sipunculus cochlearius Valenciennes, 1854:640.—Saiz Salinas, 1986b:554.

Lesinia farcimen Schmidt, 1854:2.—Selenka et al., 1883:120.

Aspidosiphon eremita Diesing, 1859:768 (not *Phascolosoma eremita* Sars, 1851).

Phascolosoma radiata Alder, 1860:75.—Southern, 1913:32.

Sipunculus heterocyathi McDonald, 1862:78–81.—Saiz Salinas, 1986b:554.

Aspidosiphon jukesii Baird, 1873:97.—Rice & Stephen, 1970:68–69.—Stephen & Edmonds, 1972:228.—Cutler & Cutler, 1979a:969–970.—Edmonds, 1980:49.—Saiz Salinas, 1986b:551.

Aspidosiphon mirabilis Théel, 1875:17; 1905:91–92.—Selenka et al., 1883:121.—Southern, 1913:31–33.

Aspidosiphon armatum Danielssen & Koren, 1880:464; 1881:64.—Selenka et al., 1883:124.—Théel, 1905:93.—Southern, 1913:31–33.

Aspidosiphon tortus Selenka et al., 1883:119–120, pl. 14, figs. 196–201.—Hérubel, 1904:564.—Fischer, 1923:21–22.—Stephen & Edmonds, 1972:236–237.—Gibbs, 1978:85.

Aspidosiphon heteropsammiarum Bovier, 1894:98.—Saiz Salinas, 1986b:555–557.

Aspidosiphon michelini Bovier, 1894:98.—Saiz Salinas, 1986b:557–559.

Aspidosiphon corallicola Sluiter, 1902:19–22.—Shipley, 1903:169–171.—Stephen & Robertson, 1952:441–442.—Cutler, 1965:58.

Aspidosiphon imbellis Sluiter, 1902:29, pl. 2, fig. 20.—Stephen & Edmonds, 1972:227–228.

Aspidosiphon inquilinus Sluiter, 1902:29–30, pl. 2, figs. 21–22.—Stephen & Edmonds, 1972:227.—Edmonds, 1980:47–49.

Aspidosiphon exhaustum Sluiter, 1912:20–21, pl. 1, fig. 11.—Murina, 1971:78.

Aspidosiphon exhaustus.—Stephen & Edmonds, 1972:224.—Murina, 1972:295–296; 1978:120.—Cutler & Cutler, 1979a:969; 1980a:4.—Edmonds, 1980:46.—Cutler et al., 1984:305.

Aspidosiphon exhaustus mirus Murina, 1974:1715–1716, fig. 2.

Aspidosiphon pygmaeus Fischer, 1921:45–47, text-figs. 1–7.—Murina, 1967a:54; 1971:78.

Paraspidosiphon pygmaeus.—Stephen & Edmonds, 1972:251–252.

Aspidosiphon kovaleskii Murina, 1964b:51–55, figs. 1–5; 1970:66.—Stephen & Edmonds, 1972:229.—Zavodnik & Murina, 1975:127.—Cutler & Cutler, 1979a:970–971.

Aspidosiphon hispitrofus LiGreci, 1980:123–134, figs. 1–4.

Material examined.—ZMUA, Sluiter's Indonesian worm (V. Si. 253); material from the Azores, 1–600 m depth collected by Zibrowius and CENTOB; Celtic Sea from P. Gibbs; French Mediterranean from Voss-Fouchart; Japan (Cutler, Cutler & Nishikawa 1984); *A. armatus*, ZMUB, type (1745); *A. corallicola*, ZMUA, types (V. Si. 1); *A. exhaustus*, MOMV, type; Cutlers' Brazilian, Japanese and Indian Ocean worms; *A. imbellis*, ZMUA, type (V. Si. 25/5); *A. inquilinis*, ZMUA, type (V. Si. 25/6); *A. jukesii*, BMNH, type (1965.25.3); Indian Ocean material (Cutler & Cutler 1979a); *A. kovaleskii*, ZIAS, type; Indian Ocean worms (Cutler & Cutler 1979a); *A. mirabilis*, ZMUB, type (15957); *A. pygmaeus*, NHRS, type specimens (279).

Discussion.—This species is the widespread, eurytopic, polymorphic member of this genus and in this way is comparable to *Golfingia margaritacea*, *Phascolion strombus*, *Sipunculus nudus*, etc. Each genus seems to have one such species with a long list of junior synonyms and a morphology difficult to define with precision. Stephen & Edmonds (1972:232–233) discuss some of the early confusion about the proper name for this taxon. Most records are from the north Atlantic Ocean and Mediterranean Sea from abandoned mollusc shells. When biologists found similar worms from different parts of the world or from different habitats, new names were put forth.

Our present concept of *A. muelleri* has an anal shield made up of very small units arranged into variable sized plates, partially separated by longitudinal furrows dorsally, in the midsection by transverse furrows, and made up of raised wart-like or cone-shaped units ventrally (Fig. 5C). The possibility that two species exist, one with pointed, cone-shaped spines on the ventral part of the anal shield and the other with only flat wart-like units, was considered. It is our conclusion that this species has the capability to respond to some environmental stimulus (e.g., pressure, temperature, or host shell shape), or that random allelic frequency shifts can occur, to produce anal shields with ventral units varying in degree of cone development.

The trunk may be straight or coiled depending on its habitat. The introvert is 1–3 times the trunk length, and there are 6–12 small nuchal tentacles. Hook morphology has been a long standing point of confusion (see Southern 1913, Stephen & Edmonds 1972:233). Our analysis of within-deme variation of compressed hooks clearly suggests that *A. muelleri* has the genetic potential for producing only unidentate hooks or only bidentate hooks or some of both on a single worm. Proximal to the rings (covering about one-third of the introvert), the scattered hooks quickly change from compressed unidentate to pyramidal. The SEM photomicrographs reveal the existence of small comb-like structures at the posterior base of the compressed hooks (Fig. 1A).

Internally the pair of introvert retractor muscles originates from the edge of the caudal shield. Under the anal shield the longitudinal muscle layer divides into separate bands. The nephridia open at or just posterior to the anus, are from 25–100% of the trunk length, and the gut forms a regular helical coil. The rectal caecum and fixing muscle are only present in some individuals.

Aspidosiphon jukesii (Baird 1873) and its several junior synonyms must be moved into this species. When one considers each char-

acter and looks not just at one author's perception but at the collected writings and the many specimens at hand, the presumed "bridgeless gap" ceases to exist. If a young worm occupies a gastropod shell in an area where solitary corals live, it is possible that this shell will be settled upon by a coral larva establishing a mutualistic relationship. This fact does not make the worm a different species. While it is true that most *A. jukesii* had anal shields with some number of cone-shaped spines, this is not universal in, or restricted to, any particular population.

The type of *A. tortus* (Selenka et al. 1883) is not with their other type specimens in the Berlin museum. They had one 25 mm worm with a longitudinal muscle layer continuous except for the anterior dorsal area where it had some separation without being clearly separate. This worm also had just one nephridium, a condition Fischer (1923) asserted was only an anomaly when he described his two worms. This has been presumed to be a separate species because it lacks unidentate hooks, now not a valid basis for separation, even if true. Their concept of spines (Stacheln) may well overlap with our idea of unidentate hooks (see their fig. 200, 201). Hérubel (1904) recorded one worm from Djibouti with no comments. When Gibbs (1978) listed this species from the Great Barrier Reef he did indicate some doubt with the (cf.) notation. Our analysis of the literature (including figures) convinces us that *A. tortus* is a junior synonym of *A. muelleri*.

When Sluiter (1902) erected *A. imbellis* he asserted that this single 13 mm worm with retracted introvert lacked hooks. Our reexamination showed this to be an error. Rings of 25–35 μm hooks exist, some with a small secondary point. The spindle muscle is attached posteriorly and it is clearly conspecific with *A. muelleri*.

Aspidosiphon inquilinis was also based on a single specimen that Sluiter (1902) differentiated from *A. muelleri* on the basis of hook and skin body morphology plus a misunderstanding of retractor origins. His spec-

imen had lived in a scaphopod shell and the anal shield has a peculiar slant. The introvert skin is folded back over the ventral edge of the anal shield. Edmonds (1980) pointed out that Sluiter had overlooked the small cone-shaped units along the shield margin just as Edmonds' four worms exhibited. These five worms have only compressed and pyramidal unidentate hooks. They are conspecific with *A. muelleri*.

In 1912 Sluiter erected *A. exhaustus* for a single 17 mm worm taken from a scaphopod shell in the east Atlantic on the slope off Morocco. No differential diagnosis was presented and examination of the type shows it to be like the other *A. muelleri* of this region with unidentate hooks. The name went unused for 59 years, after which Murina used it four times followed by the Cutlers who used it three times for cold water worms from diverse locations. This usage was predicated on the false assumption that the real *A. muelleri* must bear some bidentate hooks.

The name *A. pygmaeus* has been used by two authors. Fischer (1921) asserted that the longitudinal muscle layer consisted of bands anastomosing so frequently that he could not count them. He did say that these were most numerous at the anterior end and ran together at the posterior end. This statement caused Stephen & Edmonds (1972) to place the species in the subgenus *A. (Paraspidosiphon)*. When we examined the type material (four of his seven worms in good condition with introverts out and dorsal tentacles showing), we saw a continuous muscle layer with some fracturing under the anal shield, a condition common to many worms in this taxon. The coast of Chile is not a common location for *A. muelleri*, but Fischer's worms do fit this construct as do Murina's (1967a, 1971). Her second record was a repeat of the first for two worms from 150 m in the Gulf of Aden.

Aspidosiphon kovaleskii Murina, 1964, was presumed to differ from *A. muelleri* because it lacked bidentate hooks. Several populations (see Fischer 1895, Southern

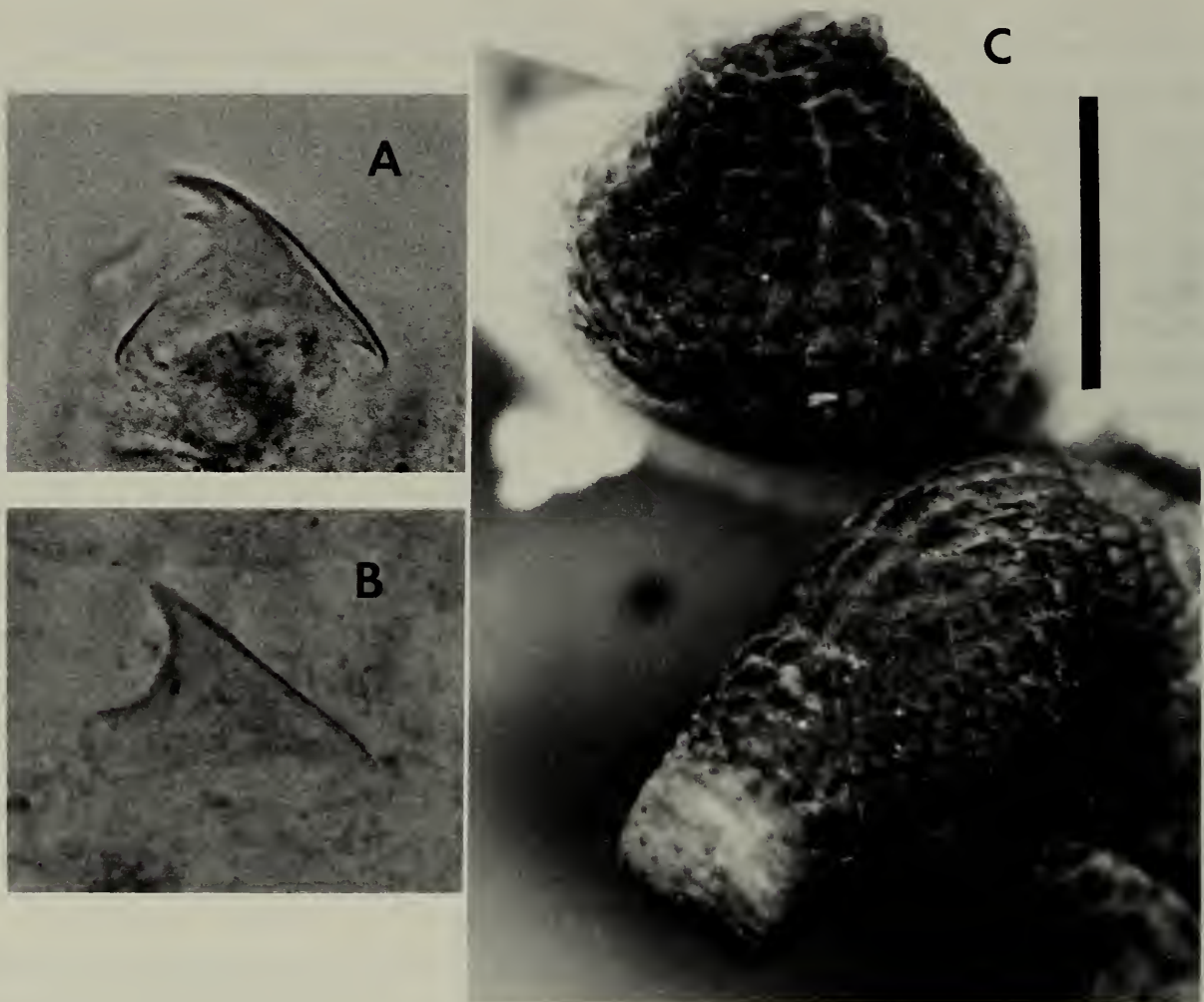


Fig. 7. *A. spiralis*: A–B, Bidentate and unidentate compressed hooks with broad bases (both 20 μm high); C, Anal shields with irregular squares in offset rows. Scale line in C = 2 mm.

1913, Gibbs 1977) of *A. muelleri* from the eastern Atlantic are reported to lack bidentate hooks. By Murina's definition these should be *A. kovalesskii*. Recently Saiz Salinas (1984:177–180) provided a detailed account of these two taxa and proposed that in both species both kinds of compressed hooks exist. He suggested that *A. kovalesskii*, if valid, might differ by having cone-shaped spines on the anal shield. He did express strong reservations about the validity of these taxa as separate and distinct biological entities; we conclude that they are not.

Aspidosiphon hispitrofus LiGreci, 1980, was based on a series of worms from Sicily. None had their introverts all the way extended, and he reported these to have no tentacles and only unidentate hooks. He did not mention the name *A. muelleri* in his

paper but compared his material to *A. clavatus*. It is clear that his material is conspecific with *A. muelleri* and his unfamiliarity with the phylum led him to misinterpret the distal end of the introvert.

Distribution. — Common in the northeast Atlantic from Norway through the British Isles, the Azores and Canary Islands and West Africa (to 10°N). It extends through the Mediterranean and Red Sea into the Gulf of Aden and along the coast of east Africa to Madagascar and South Africa. The records then skip to Ceylon and sparse reports up to Japan through Thailand, Vietnam, Indonesia, and down to Australia, New Guinea, and Kermadec Island. Most of the Pacific Ocean is unpopulated by this species. One record from Juan Fernandez Island off Chile (33°S) and one from southern Brazil

(34°S) exist, but nothing else from the American hemisphere. This southern hemisphere distribution is intriguing. Throughout most of its range this species inhabits shelf depths (10–300 m), but there are several records down to 1000 m with the deepest at 2930 m.

Aspidosiphon spiralis Sluiter, 1902

Aspidosiphon spiralis Sluiter, 1902:25–26, pl. 2, figs. 9–13.—Shipley, 1903:171.—Stephen & Edmonds, 1972:236.

Material examined.—ZMUA, type specimens (V. Si. 171–174).

Discussion.—While Sluiter said this species has unidentate hooks, rings of small bidentate hooks are also present. These are about 20 μm high and the secondary point is not large (Fig. 7A, B). The unidentate hooks are about the same size and in rings. A gradual transition may exist during growth as there are some intermediate hooks. The anal shield does not have regular furrows, but neither is it made up of uniform granules. It is divided into irregular squares overlain with horny protein (Fig. 7C). The retractor muscles originate from the posterior end of the trunk. This species does not have a firm foundation (four worms), but we propose no change in its status at this time.

The three worms Shipley identified cannot be located, and we question whether he was looking at the same entity. His description of the agglutinated sand packed around the opening of the gastropod shell is much more typical of *Phascolion* species. Also, he provided no morphological information (other than color) or station data.

Distribution.—Indonesia, gastropod shells, 14–91 m.

Subgenus

Aspidosiphon (Paraspidosiphon)

Diagnosis.—Introvert with compressed hooks in rings, longitudinal muscle layer divided into anastomosing bands. All bore in coral or rock.

Aspidosiphon coyi Quatrefages, 1865

Aspidosiphon coyi Quatrefages, 1865:608–609 (partim).—Baird, 1868:101.—Stephen & Edmonds, 1972:340.—Saiz Salinas, 1984:42–49.

Phascolosoma truncatum Keferstein, 1867:50–53, pl. 6, figs. 15–18.

Aspidosiphon truncatus.—Selenka et al., 1883:118–119.—Selenka, 1885:20.—Sluiter, 1898:444; 1902:17.—Shipley, 1899b:154; 1902:132.—Hérubel, 1904:564.—Ikeda, 1904:38–39.—Lanchester, 1905a:34.—Fischer, 1914b:15.—Benham, 1912:136.—Hammerstein, 1915:2.—Sato, 1939:428.—Cutler & Cutler, 1979a:976.—Cutler et al., 1984:309–310.

Paraspidosiphon truncatus.—Stephen & Edmonds, 1972:258.

Material examined.—MNHN, type material (V20); *A. truncatus*, ZMUA, Sluiter's Indonesian worm (V. Si. 25.1); from Mozambique (Cutler & Cutler 1979a) and Japan (Cutler et al. 1984); USNM, unpublished material from the Gulf of Panama (21477), and Gulf of California, Puerto Penasco, Mexico (26443).

Discussion.—*A. coyi* is one of two species in this subgenus with a grooved anal shield. The primary distinction from *A. laevis* is the presence of distal rings of bidentate hooks 25–35 μm tall. However, the secondary tooth on these is very small and not consistently present. There can be unidentate compressed hooks as well as thin pyramidal hooks, and the presence of both has led to some confusion in the literature. The skin papillae towards the two ends of the trunk are large and rugose. The longitudinal muscle layer can exhibit much anastomosing and is not always clearly banded. The retractors originate from the posterior end (95–100%), the spindle muscle may bifurcate near the anus, and the wing muscle is well developed extending down to near the ventral nerve cord. The nephridia are 40–95% of the trunk length and attached for most of their length. This has not been a

well defined species and the size of the data base is small. Striking similarities to *A. (Aspidosiphon) muelleri* exist (e.g., shield, retractors, hooks), and show another example of the less than clear boundary between the two subgenera.

The careful redescription of this species by Saiz Salinas (1984) brought the name *A. coyi* back from its earlier dubious status (Stephen & Edmonds 1972) and these taxa are clearly conspecific. The location of Quatrefages' specimens is not clear but is probably somewhere in the Indian Ocean.

Distribution.—Several locations in the western Indian Ocean and the western Pacific from Japan through Okinawa, Philippines, Indonesia, and Kermadec Islands. Two Latin American records of uncertain location exist: The type of *A. truncatus* from Panama (east or west coast?) and a single 3 mm worm from San Salvador (Bahamas or Galapagos?). Eastern Pacific locations for these two are supported by the USNM material from the Gulf of Panama and the Gulf of California. The former was collected in 1866 and may be part of Keferstein's type collection.

Aspidosiphon fischeri ten Broeke, 1925

Aspidosiphon fischeri ten Broeke, 1925:92–93, figs. 21–22.—Migotto & Ditadi, 1988: 250–251.

Paraspidosiphon fischeri fischeri.—Stephen & Edmonds, 1972:244–245.—Amor, 1975:118–119.—Rice, 1975:38–44.—Rice & Macintyre, 1979:311–319.

Aspidosiphon fischeri cubanus Murina, 1967b:39–42, figs. 5–7, 1967c:1331.

Paraspidosiphon fischeri cubanus.—Stephen & Edmonds, 1972:245.

Material examined.—ZMUA, type material (V. Si. 5); USNM, Venezuelan specimens identified by M. Rice (100901); unpublished specimens labeled *A. truncatus* (20726, 20725, 20727, 20836); our 1988 collections from the Caribbean.

Discussion.—The body wall of these small

worms (trunks 4–16 mm) is smooth, thin, and white, but the longitudinal muscle bands cannot be easily seen through it, making it easy to misplace these worms in *A. (Aspidosiphon)* during preliminary sorting, i.e., they are similar to *A. A. misakiensis* or *A. A. gosnoldi*. Few, thin, ill-defined muscle bands exist that anastomose frequently and seem to fuse in the posterior part of the trunk in some worms. The long introvert (one or two times the trunk) bears rings of compressed, 18–27 μm , bidentate hooks. The proximal rings may include hooks with a very small secondary point and unidentate hooks mixed together or a few rings of just unidentate hooks. Following these are scattered, pale, pyramidal hooks 15–50 μm tall. The retractor muscles are thin and originate at or very near the posterior end of the trunk (95–100%). The nephridia are short; 33–50% of the trunk length.

When ten Broeke described this species she provided no differential diagnosis, and the differences from other species, e.g., *A. parvulus*, or those mentioned above, are not always distinct. One might make a case for this being a subspecies or an incipient or sibling species, but we propose no change now. Migotto & Ditadi (1988) question the basis for the subspecies *A. fischeri cubanus* Murina, 1967, and we agree that it only represents some of the variation within the species.

Distribution.—Numerous southern Caribbean locations from Cuba to Sao Paulo, Brazil, in shallow coral rock. Also from the Pacific coast of Panama, Ecuador, plus James and Hood Islands, Galapagos.

Aspidosiphon laevis Quatrefages, 1865

Aspidosiphon laevis Quatrefages, 1865: 609.—Baird, 1868:102.—Vaillant, 1871: 272–273; 1875: pl. 4, figs. C1–4.—DeRochebrune, 1881:233.—Saiz Salinas, 1984:55–62.

Aspidosiphon laevis.—Stephen & Edmonds, 1972:340.

Aspidosiphon cumingii Baird, 1868:102, pl.

- 11, fig. 2.—Selenka et al., 1883:113–115.—Fischer, 1892:85; 1922b:12.—Collin, 1892:177.—Sluiter, 1898:444; 1902:17.—Augener, 1903:321–322.—Hérubel, 1904:564.—Monro, 1931:34.—Leroy, 1936:426.—Andrew & Andrew, 1953:1.—Rice & Stephen, 1970:67.—Cutler, 1973:179–180.
- Paraspidosiphon cumingii*.—Stephen & Edmonds, 1972:243–244.—Edmonds, 1980:50.
- Aspidosiphon major* Vaillant, 1871:270–271; 1875: pl. 4, figs. A1–6.—De-Rochebrune, 1881:232.
- Aspidosiphon klunzingeri* Selenka et al., 1883:115–116, pl. 13, figs. 187–189.—Fischer, 1896:338; 1914a:70.—Sluiter, 1898:444; 1912:20.—Shipley, 1898:471; 1899b:153.—Hérubel, 1904:564.—Monro, 1931:34.—Edmonds, 1956:308.—Wesenberg-Lund, 1957b:8–9; 1959a:196; 1959b:211–212; 1963:138.—Cutler & Cutler, 1979a:974–975; 1979b:107.
- Paraspidosiphon klunzingeri*.—Stephen & Edmonds, 1972:247–249.—Rice & Macintyre, 1972:42.—Rice, 1975:40–41.—Haldar, 1976:7.—Gibbs, 1978:85.
- Aspidosiphon gigas* Sluiter, 1884:39–57, pl. 2, figs. 1–11, pl. 2a, figs. 12–25; 1886:473; 1891:116; 1902:19.
- Paraspidosiphon gigas*.—Stephen & Edmonds, 1972:246.
- Aspidosiphon angulatus* Ikeda, 1904:45–47, figs. 11, 78–80; 1924:37.—Sato, 1939:428.—Cutler & Cutler, 1979a:974; 1981:81.—Cutler et al., 1984:308.
- Paraspidosiphon angulatus*.—Stephen & Edmonds, 1972:241.
- Aspidosiphon speciosus* Gerould, 1913:426–427, text-fig. 16, pl. 62, fig. 22.—Fischer, 1922c:13.—Migotto & Ditadi, 1988:254–257.
- Paraspidosiphon speciosus*.—Stephen & Edmonds, 1972:253.—Rice, 1975:38–45.—Rice & Macintyre, 1979:314.
- Aspidosiphon grandis* Sato, 1939:414–419, pl. 21, fig. 21, text-figs. 46–50.—Cutler & Cutler, 1981:83–84.
- Paraspidosiphon grandis*.—Stephen & Edmonds, 1972:246–247.
- Aspidosiphon grandis obliquoscutatus* Murina, 1974:1713–1715, fig. 1.
- Aspidosiphon pachydermatus* Wesenberg-Lund, 1937:9–16, text-figs. 4–9.
- Paraspidosiphon pachydermatus*.—Stephen & Edmonds, 1972:250–251.
- Aspidosiphon brasiliensis* Cordero & Mello-Leitao, 1952:277–282, 288–292, text-figs. 1–5.
- Paraspidosiphon brasiliensis*.—Stephen & Edmonds, 1972:241–243.
- Aspidosiphon johnstoni* Edmonds, 1980:51–53, figs. 91, 100–102.—Lopez et al., 1984:194–196.
- Aspidosiphon quatrefagesi* Saiz Salinas, 1984:49–55, fig. 4.
- Material examined*.—MNHN, type material (V20); our 1985 Hawaii and 1988 Venezuela material; *A. cumingii*, type no longer at BMNH; *A. angulatus*, Madagascar and Polynesia (Cutler & Cutler 1979a); *A. brasiliensis*, type cannot be located; *A. gigas*, ZMUA, holotype (V. Si. 8); *A. grandis*, ZITU, type specimen (24); *A. johnstoni*, two specimens from Edmonds' original material; *A. klunzingeri*, type cannot be located; ZMUA, Sluiter's Durban worm (V. Si. 9); UZMK, Wesenberg-Lund's Cape Verde material; South Africa and Cape Verde (Cutler & Cutler 1979a, b); USNM, 26437 from Saipan identified by W. K. Fisher; *A. pachydermatus*, the type cannot be located; USNM, two specimens identified by W. K. Fisher (from Saipan, 24645 and Philippines, 21480); *A. speciosus*, USNM, type material (16820, 16391, 4088); two specimens from Brazil (Migotto & Ditadi, 1988).
- Nomenclatural note*.—Quatrefages' original spelling is incorrect (Steyskal, pers. comm.) and when the correct ending is appended the name *A. levis* Sluiter becomes a junior homonym according to ICZN Art. 58.
- Discussion*.—*A. laevis* is a widespread but low density population of worms that has

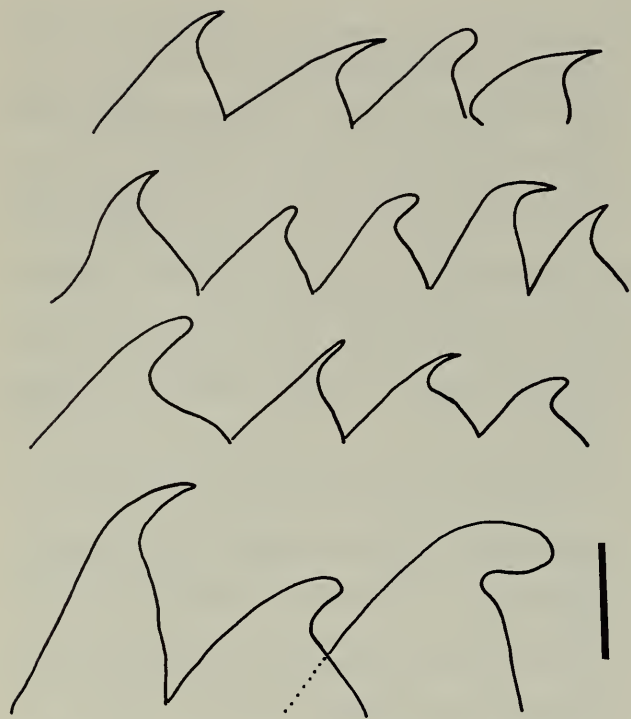


Fig. 8. Unidentate, compressed, Type A hooks of several *A. laevis* from different populations to show differences in shape and size, the latter being roughly correlated with trunk size. Scale line = 40 μm .

been given several names over the past century. One of the characters that has been weighted very differently by various authors is the nature of the caecum and its elaborations as discussed above. Setting this aside, a second issue has been the presence/absence of introvert spines. It is clear that when a few authors made reference to spines, they were either looking at scattered unidentate compressed hooks, or had a different species in hand. These worms have a solid anal shield bearing 10–15 longitudinal grooves. They have unidentate, compressed hooks, sharply pointed or blunt, in many rings (Fig. 8). These are 20–80 μm tall, hook size being roughly correlated with trunk size. Also present are a few scattered compressed hooks (referred to as spines by some earlier authors). Up to 24 tentacles surround the nuchal organ.

Internally, the pair of retractor muscles are fused for most of their length, sometimes giving the impression of a single broad muscle with the ventral nerve cord running through a notch in the base. These muscles

usually have their origins from the body wall about 65–80% of the distance towards the posterior end of the trunk, i.e., well in front of the caudal shield. Another distinctive feature is the bifurcation towards the anterior end of the spindle muscle. One branch continues along the rectum into the connective tissue and wing muscle to join the body wall just anterior to the anus. The second, and often larger branch, leaves the posterior rectum going to the dorsal body wall well posterior to the anus. In many specimens the contractile vessel is not a smooth tube but has vesicular pouches or swellings along the part of its length united with the retractors (not unlike that seen in some *Golfingia* specimens, and sometimes confused with contractile vessel villi [see Cutler & Cutler 1987:750]). The rectum usually bears a caecum that may be simple or complex (see part 8, Morphological Characters section). The 25–35 longitudinal muscle bands anastomose frequently, and the circular muscle layer also subdivides into anastomosing bundles of varying degree of development. The nephridia open at, or just posterior to, the anus, are attached to the body wall for about half to two-thirds their length, and are usually more than half the trunk length.

The unpublished USNM material (21480 and 24645) consists of two worms, 44 and 123 mm long. They both have complex multiple caeca, a grooved anal shield, unidentate hooks (in the larger one these are blunt triangular and up to 60 μm tall), and in all ways match *A. laevis*.

This new arrangement reduces ten putative species to the rank of junior synonyms of *A. laevis*, a decision reached only after extended analysis. We shall not detail each case, but in a few instances there were observational errors made by the original author (for example, *A. gigas* does have rows of unidentate hooks, a spindle muscle and a complex rectal caecum, all overlooked by Sluiter). However, in most cases the different conclusions are based on judgments

about within-deme variation, or simply lack of either critical comparison or differential diagnoses (e.g., Gerould [1913:427] when describing *A. speciosus* simply says: "This species resembles *A. klunzingeri* from the Red Sea" and nothing more as to how it differed). In another case Saiz Salinas (1984) erected *A. quatrefagesi* based on a suite of characters he assumed to be absent in older species while actually they were present but simply not mentioned by earlier authors.

As discussed in the Morphological Characters section, the variability in rectal appendages is great, therefore, to use such a variable character to differentiate species is unwise. A more difficult issue for us, partly because of statements by Edmonds (1980) and Rice (1975), centers on the hook morphology. We have examined many hooks from museum specimens and newly collected material, comparing hooks from small worms to those from large ones, and hooks from anterior to posterior rings in the same worm (Fig. 8). We conclude that while populations do exhibit among-deme differences, much of the alleged between species variation in shape is present within demes. Therefore, hook shape alone cannot be used to separate these putative species.

Distribution. — Widespread, but low density, in warm water Indo-West Pacific Ocean (Durban to the Red Sea, Andaman Islands, Malaya to southern Japan, Indonesia, Great Barrier Reef and several islands out to Hawaii). Also present in the Caribbean and west Atlantic (from 20°S to 31°N), then in the east Atlantic from the Canary and Cape Verde Islands to the Gulf of Guinea. Inhabits shallow water coral rock.

Aspidosiphon tenuis Sluiter, 1886

Aspidosiphon tenuis Sluiter, 1886:491–492, pl. 3, fig. 7; 1891:116; 1902:19.

Paraspidosiphon tenuis. — Stephen & Edmonds, 1972:257.

Aspidosiphon levis Sluiter, 1886:493–494, pl. 3, fig. 8; 1891:116; 1902:18.

Paraspidosiphon levis. — Stephen & Edmonds, 1972:249–250.

Aspidosiphon ambonensis Augener, 1903:325–328, figs. 5–8.

Aspidosiphon steenstrupii var. *ambonensis* Fischer, 1922a:24–26; 1923:21.

Paraspidosiphon ambonensis. — Stephen & Edmonds, 1972:240–241.

Aspidosiphon formosanus Sato, 1939:421–424, pl. 21, fig. 23, text-figs. 55–57. — Cutler & Cutler, 1981:81–83.

Paraspidosiphon formosanus. — Edmonds, 1971:144–146; 1980:50–51. — Stephen & Edmonds, 1972:245.

Aspidosiphon havelockensis Haldar, 1978:37–41, figs. 1–2.

Aspidosiphon speculator. — Cutler & Cutler, 1979a:975–976 (partim).

Material examined. — BMNH, (1889.6.15.42/44) syntype; *A. levis*, ZMUA, type material (V. Si. 11); *A. ambonensis*, MNHU, type material (6956–6958); *A. formosanus*, type material cannot be located, but we have examined material from Guam and Australia identified by S. J. Edmonds; *A. speculator*, Pacific Ocean (Cutler & Cutler 1979a).

Discussion. — *A. tenuis* is here defined as having an anal shield made up of very fine dark units with a smooth overall appearance; a few very short grooves may appear around the margin. The distal rings of bidentate hooks (30–60 μm tall) lack the distinct tongue on the clear streak (Fig. 2C) and are followed by scattered, unidentate hooks (25–60 μm tall) with an internal clear streak in the distal ones. More proximally, these scattered unidentate structures have lateral reinforcing ridges. Dark pyramidal or conical hooks are absent. Internally this species is very much like *A. steenstrupii* except that only two of the ten worms dissected has a rectal caecum and the nephridia are less than 50% of the trunk length.

When Sluiter (1886) described this species he overlooked the distal rings of bidentate hooks and posterior attachment of the spin-

dle muscle. He overemphasized the few small grooves around the margin of the anal shield. The caudal shields are not all distinctly grooved. Therefore, this is clearly conspecific with *A. levis* from the same location, and becomes the senior synonym by virtue of their position in the text.

Fischer (1922a) reduced *Aspidosiphon ambonensis* to a variety of *A. steenstrupii*, but Stephen & Edmonds (1972) elected to elevate it back to species rank since the shape of the clear area in the hook "seems to be different." We assume they based their conclusion on Augener's (1903) picture (their fig. 29K is Augener's fig. 6). Our examination of the type material (19 worms) confirms Augener's perceptions and supports our position that this population is conspecific with *A. tenuis*, but different than *A. steenstrupii* in accordance with Stephen & Edmonds (1972).

Sato (1939) erected *A. formosanus*, but Cutler & Cutler (1981) reduced it to a junior synonym of *A. steenstrupii*. Given our current understanding we would move *A. formosanus* into the synonymy of *A. tenuis* as it shares its attributes.

In 1978 Haldar described *Aspidosiphon havelockensis*. In his unpublished dissertation (pers. comm.) it is reduced to a junior synonym of *A. steenstrupii ambonensis* differentiated from the nominate form on the basis of hook, spine, and papillae structure. We agree with his conclusions as far as they go. However, we now consider both these names to be junior synonyms of *A. tenuis*.

Upon reexamination, the specimens Cutler & Cutler (1979a) identified as *A. speculator* from the Solomon Islands and Thailand belong in this taxon.

Distribution.—Andaman Islands to Thailand, Formosa, and Guam, out to the eastern Caroline Islands and down through the Solomon Islands to the Great Barrier Reef and Indonesia.

Aspidosiphon parvulus Gerould, 1913

Aspidosiphon parvulus Gerould, 1913:425–426, pl. 61, fig. 17, text-fig. 15.—Stephen

& Edmonds, 1972:233–234.—Cutler, 1973:178–179.

Aspidosiphon spinoso-scutatus Fischer, 1922c:13–14, text-figs. 2–3.—Murina, 1967b:42; 1967c:1332.

Paraspidosiphon spinososcultatus.—Stephen & Edmonds, 1972:254.—Rice, 1975:38–45.

Material examined.—USNM, type (15118); western north Atlantic (Cutler 1973); our 1988 Venezuelan worms; *A. spinoso-scutatus*, MNHU, type (6053).

Discussion.—This species shares many attributes with *A. fisheri*, but the shield morphology seems consistent and distinctive. Centrally it is made up of larger flat plates; these are sometimes arranged in rows giving an impression of ridges and grooves. Ventrally and laterally the units become smaller, scattered, wart- or cone-shaped. The shields have a diffuse boundary where the units grade into coarse trunk papillae. At both ends of the trunk these darker papillae are located in rectangles that remind one of *Sipunculus* skin. The hooks (bidentate and unidentate in rings, scattered unidentate, and pyramidal, Fig. 1E) are 25–35 μm tall. The 10–12 short tentacles may appear webbed together with connective tissue, and there are about 24 anastomosing longitudinal muscle bands. These bundles are generally quite distinct in worms over 5 mm long, more so towards the anterior end (see Cutler 1973:178 where Gerould's 3 and 4 mm specimens are discussed). The nephridia are 50–75% of the trunk length.

Distribution.—Western Atlantic Ocean from Cape Hatteras through the Caribbean to Venezuela; often found together with *Themiste alutacea* and *Nephasoma pellucidum* in branching corals.

Aspidosiphon planoscutatus

Murina, 1968

Aspidosiphon planoscutatus Murina, 1968:1722–1724, figs. 1–2; 1971:78.

Material examined.—ZIAS, type material.

Discussion.—This taxon is based on two specimens and is very similar to *A. steenstrupii* but has only unidentate compressed hooks on the introvert. Also, the shield units are smaller (fine grained like *A. zinni*) and the trunk is densely covered with more obvious skin bodies. The nephridia are 85% of the trunk length.

The Red Sea is a marine habitat with unusual abiotic conditions (e.g., high salinity, low oxygen, high temperature) that may restrict gene flow and favor selection of different allelic frequencies. The absence of bidentate hooks on the introvert may be a real difference, but we cannot verify this. Despite our reservations we are leaving the name because of the habitat. It is hoped that more collecting in the area will produce additional material for analysis.

Distribution.—Red Sea at 40 m.

Aspidosiphon steenstrupii
Diesing, 1859

Aspidosiphon steenstrupii Diesing, 1859:767, pl. 2, figs. 1–6.—Quatrefages, 1865:610.—Selenka et al., 1883:116–118.—Sluiter, 1886:489–490; 1891:115; 1902:18.—Whitelegge, 1899:394.—Shipley, 1899b:153–154; 1902:131–132; 1903:171.—Ikeda, 1904:40–41; 1924:38.—Hérubel, 1904:564.—Lanchester, 1905b:39.—Fischer, 1914a:70–71; 1914b:13; 1922a:23; 1922c:13; 1923:21; 1926:108; 1931:139.—ten Broeke, 1925:93–94.—Monro, 1931:34.—Sato, 1935:315–316; 1939:424–426.—Leroy, 1936:426; 1942:36–38.—Stephen, 1942:253.—Stephen & Robertson, 1952:441.—Edmonds, 1956:307–308.—Wesenberg-Lund, 1959a:197–198; 1963:138.—Murina, 1967b:42; 1981:12–13.—Cutler, 1977a:148.—Cutler & Cutler, 1979a:976; 1979b:107–108.—Cutler et al., 1984:308–309.—Migotto & Ditadi, 1988:259–260.

Paraspidosiphon steenstrupii steenstrupii.—Stephen & Edmonds, 1972:254–255.—Rice, 1975:38–45.—Haldar, 1976:8.—Rice & Macintyre, 1972:42; 1979:311–319.—Edmonds, 1980:51.

Aspidosiphon steenstrupii var. *faciatus* Augener, 1903:322–325, figs. 1–4.

Paraspidosiphon steenstrupii fasciatus.—Stephen & Edmonds, 1972:255–256.

Aspidosiphon fuscus Sluiter, 1881:86–108; 1886:474; 1891:116; 1902:19.—Selenka et al., 1883:116.

Aspidosiphon semperi ten Broeke, 1925:92, text-figs. 18–20.—Gibbs & Cutler, 1987:56.

Paraspidosiphon semperi.—Stephen & Edmonds, 1972:252.

Aspidosiphon speculator Selenka, 1885:19–20, pl. 4, figs. 24–27.—Fischer, 1914b:71; 1920:413.—Wesenberg-Lund, 1959b:213.—Cutler & Cutler, 1979a:975–976 (partim).—Not Saiz Salinas, 1986a:11–14.

Paraspidosiphon speculator.—Stephen & Edmonds, 1972:253–254.

Aspidosiphon makoensis Sato, 1939:419–421, pl. 21, fig. 22, text-figs. 51–54.—Cutler & Cutler, 1981:82–83.

Paraspidosiphon makoensis.—Stephen & Edmonds, 1972:250.

Aspidosiphon trinidadensis Cordero & Mello-Leitao, 1952:283–286, 292–294, figs. 6–10.—Cutler & Cutler, 1979b:108; 1980c:206.

Paraspidosiphon trinidadensis.—Stephen & Edmonds, 1972:257–258.

Aspidosiphon exostomum Johnson, 1964:331–332, pl. 7.

Paraspidosiphon exostomus.—Stephen & Edmonds, 1972:244.

Aspidosiphon ochrus Cutler & Cutler, 1979a:976–979, figs. 15–17.—Edmonds, 1987:204.

Material examined.—ZMUA, Sluiter's 1902 specimens (V. Si. 21); our Pacific and Caribbean material; Brazil (Migotto & Ditadi 1988); *A. semperi*, ZMUA, types (V. Si. 14); *A. exostomum*, RSME, type (1965.32.2); *A. speculator*, BMNH, 1885. 12.3.28, syntype; specimens from Canary Islands and Spain identified by J. Saiz Salinas; Madagascar (Cutler & Cutler 1979a).

Discussion.—We came to the present understanding of *A. steenstrupii* only after

looking at many worms from diverse locations, and carefully reexamining the literature. The color of the anal shield was a confusing element. It now seems clear that a range of colors is possible, from almost white to very dark brown, and that additional calcareous material may be deposited externally, thus masking the underlying units. Geographic variation seems present with the Atlantic Ocean populations being dark, the mid Pacific Ocean populations being pale and the Indian Ocean populations exhibiting a mixture (a higher frequency of dark shields in populations near continents, rare in island populations).

The other major issue centers around the hooks. We are defining this species as having bidentate hooks in rings (30–60 μm tall; up to 90 μm in worms over 25 mm long), most with a tongue-like extension on the internal clear streak (Fig. 2B), and no unidentate compressed hooks. The proximal introvert does bear many scattered, dark, pyramidal hooks about 30–60 μm tall.

Internally the pair of retractor muscles originate about 70–85% of the distance to the posterior end of the trunk, not correlated with trunk size (see Table 2). The nephridia are commonly 50–80% of the trunk length and attached to the body wall for 50–75% of their length (over 90% in three worms). A simple rectal caecum was observed in 21 of the 30 worms dissected. The longitudinal muscle bands anastomose (14–22 anteriorly and 20–28 posteriorly), and the number is not correlated with trunk length.

J. Silverstein (pers. comm.) determined the karyotype on a Japanese population. The 2N number is 20 with five pairs of meta/submetacentric and five pairs of telo/subtelocentric chromosomes.

When Selenka (1885) erected *A. speculator* he made no reference to any other species (no differential diagnosis or key). In Stephen & Edmonds (1972) the key separates these two species based on the location of the retractor origins that were imprecisely stated in the original. In the syntype, the

origins are at 75% of the distance to the posterior end of the trunk, well within the *A. steenstrupii* range. The internal structure of the compressed hooks and the nature of the pyramidal hooks, shield, and other characters all match this species. The part of Cutler & Cutler (1979a) collection that belongs here are the Madagascar worms, the remainder are *A. tenuis*. Saiz Salinas (1986a) used *A. speculator* for a collection that we consider to be *A. misakiensis*.

Fischer (1922a) reduced Augener's 1903 *A. steenstrupii fasciatus* to a junior synonym of the nominate form where it remained until Stephen & Edmonds (1972) resurrected its subspecies rank. They based their decision on the clear area in the hook and color differences on the shield and mid-trunk. Our examination of the type, within the context of this study, convinces us that Fischer's action was correct.

When ten Broeke (1925) described *A. semperi* from Curacao she asserted that it had four retractor muscles, but Gibbs & Cutler (1987:56) determined that there are only two. Despite the pale colored anal shield *A. semperi* is clearly conspecific with *A. steenstrupii*, a conclusion confirmed by our recent collections in Curacao.

Sato's two species, *Aspidosiphon formosanus* and *A. makoensis* were reduced to the status of junior synonym in Cutler & Cutler (1981). We reaffirm that action for the latter but not the former (see below).

Aspidosiphon trinidensis was described from a single worm that cannot be located. The two subsequent reports were also based on single worms (in Cutler & Cutler 1980c, it should have read 25 mm trunk, not 125 mm). Reexamination of the two available worms revealed a few distal rings of bidentate hooks that had been overlooked. Those structures reported as unidentate hooks are now interpreted as pyramidal hooks. Cordero & Mello-Leitao's worm (1952) had its introvert entirely withdrawn and the objects they described as unidentate hooks were not in rings. From their words and drawings we

interpret these as pyramidal hooks. With this understanding (and the assumption that they too overlooked the bidentate hooks) nothing separates *A. trinidadensis* from *A. steenstrupii*, thus we place it in synonymy.

Aspidosiphon exostomus (Johnson 1964) was alleged to be different because of the dorsal crown of tentacles. This was clearly visible as the esophagus was protruding through the mouth. However, we now know that all members of the Aspidosiphonidae have dorsal tentacles and this taxon is clearly not unique.

When Cutler & Cutler (1979a) described *A. ochrus* we were working within a different experiential framework. As a result of the present analysis, it clearly should be reduced to a junior synonym. In that same paper we identified a specimen from Madagascar as *A. speculator* that, upon reexamination, we now consider to be an *A. steenstrupii*. Edmonds (1987) used the name *A. ochrus* after consulting with us, but these also are *A. steenstrupii* with pale anal shields.

Distribution.—Throughout the western and northern Indian Ocean, Queensland through Indonesia and the South China Sea to southern Japan, out through the western Pacific islands to Hawaii. Also collected from numerous Caribbean locations, in the eastern Atlantic only from the Cape Verde Islands and the Gulf of Guinea. It lives in shallow water coral rocks.

Zoogeographical Summary

Ten of the 19 species live in the tropical/subtropical western Atlantic Ocean and Caribbean Sea, an area bounded by Cape Hatteras on the north and the Amazon delta on the south (*A. albus*, *A. exiguus*, *A. gosnoldi*, *A. parvulus*, *A. fischeri*, *A. mexicanus*, *A. elegans*, *A. laevis*, *A. steenstrupii*, and *A. misakiensis*). The first four of these are endemic to the region. The fifth extends into the eastern Pacific (Panama to Galapagos). The sixth extends its range in the other direction, to the eastern Atlantic (between Iberia and

the Gulf of Guinea) but nowhere else. The next three species are circum-tropical while the last is found on both sides of the Atlantic Ocean and off Japan and Australia.

Two species are found in the eastern Atlantic and elsewhere that do not live in the western part (*A. venabulus* from both sides of Africa, and *A. muelleri*, see below). Also in the north Atlantic (plus one record from the Mozambique Channel) is *A. zinni*, the one bathyal/abyssal member of this genus.

Of special note is *A. muelleri*, since it has the most widespread distribution, almost cosmopolitan in temperate waters. Two apparent gaps occur; in the western Atlantic (except for one record off southern Brazil), and in the eastern Pacific there is only one record off Chile. This is the most eurytopic *Aspidosiphon* living in a much wider variety of temperatures and depths than other species.

Six species are widely distributed within the Indo-West Pacific area. *Aspidosiphon gracilis schnehageni* and *A. coyi* extend into the eastern Pacific Ocean. Three are also found in the Caribbean (as above). The remaining two do not get to Hawaii or the Atlantic (*A. gracilis gracilis* and *A. tenuis*). Two species (*A. thomassini* and *A. spiralis*) are more restricted within the Indian Ocean and *A. planoscutatus* is known only from a single collection in the Red Sea.

Of particular interest is the number of endemic species in the warm water Atlantic/eastern Pacific Ocean (six) when compared to the Indo-West Pacific area (five). Of the 19 species, 13 live somewhere in the Atlantic Ocean while 11 occupy some part of the Indo-West Pacific (six of these are in both areas). These data have interesting evolutionary implications suggesting that the traditional "center of origin" hypothesis for marine invertebrates (Indo-West Pacific) may not fit *Aspidosiphon*.

While it is true that common, widespread species bore in coral or soft rock, 11 species (58%) do not occupy this stereotypical aspidosiphonid niche, i.e., they live in dis-

carded mollusc shells (8), arenaceous foraminiferan tests (1), or interstitially (2).

Acknowledgments

The encouragement and exchange of ideas and specimens with S. J. Edmonds, Adelaide, has contributed greatly to the completion of this work. A working visit from J. Saiz Salinas, Bilbao, including an open exchange of perceptions, was very fruitful. The opportunity to read unpublished manuscripts and to examine some specimens of A. E. Migotto and A. S. F. Ditadi, Sao Paulo, and B. P. Haldar, Calcutta, has added significantly to our understanding. Our work in Hawaii was accomplished with the assistance of B. Burch, Bishop Museum and M. Hadfield, Kewalo Marine Laboratory. The field work in Curacao was dependant on the cooperation of W. Bakhuis, Carmabi Foundation. In Cumana J. Perez and associates at the Universidad de Oriente assisted us in many ways. The visit to the Fundacion Cientifica Los Roques was made possible by the cooperation of R. Laughlin and B. Alvarez. Lynn Cutler, Mountain View, and J. Silverstein, Seattle, provided invaluable assistance in the field and lab. Correct spelling of species' names was kindly provided by G. Steyskal, Washington, and K. Bart, Clinton, assisted with the scanning electron microscope. Financial support was provided by the National Science Foundation (BSR 86-15315).

The cooperation of the following persons and institutions in the loan of reference material and/or providing access to their collections was essential to the completion of this project and greatly appreciated: E. Easton (BMNH); J. Rénaud-Mornant (MNHN); G. Hartwich (MNHU); C. Carpine (MOMV); R. Oleröd (NHRS); S. Chambers (RSME); M. Rice (USNM); J. Kirkegaard (UZMK); A. Ivanov (ZIAS); Zoological Institute Tohoku University, Sendai; A. Pierrot-Bults (ZMUA); E. Willassen (ZMUB); M. Dzwillo (ZMUH).

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